

The function of the mobbing-like response to secondary predator cues in wild meerkats



Submitted by Isabel May Driscoll to the University of Exeter as a thesis for the degree of *Masters of Science by Research Biological Sciences*, September 2019

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(Signature) *Isabel May Driscoll*

Acknowledgements

I'd like to start by saying a huge thank you to my primary supervisor Alex Thornton for always being kind, supportive and generally amazing. For making it feel as though a weight had been lifted after every meeting no matter how small or large an issue was. Alex's guidance and insight has been truly invaluable in helping me develop and express my thoughts throughout this process. Thank you to my supervisor Marta Manser for allowing me the great privilege to work with the meerkats. For providing brilliant expertise on the species she has spent the last 20 years studying and for instrumental advice and discussion on experimental design and the writing of this thesis.

Thank you to all of the volunteers and researchers that have contributed to the meerkat project over the last 2 decades, without which this thesis would not have been possible. Special thanks to Tim Clutton-Brock for establishing the project on such a fascinating study system. Thank you to Dave Gaynor, Tim Vink, Jacob Brown and Coline Muller for running the project during my time in the field, giving great advice, helpful discussion, logistical support and helping me find my feet at the project. Additional thanks to Tim Vink for maintaining the database and aiding in the acquisition of cat urine from the very bemused local vets. Thank you to everyone at the KRC during my time there for filling evenings with laughter, watching stunning sunsets, dressing up with spectacular creativity at any and every opportunity, and for keeping me sane in spite of the trials of desert life.

Thank you to all the jackdaw group for welcoming me as an honorary group member, for giving statistics advice, welcome breaks, laughter and a never ending supply of biscuits. Huge thanks to Flora Rendell-Bhatti and Tanya Payne for providing constant support and adventures. Finally, the biggest thank you of all to my parents, Polly Strauss and Adrian Driscoll, for being there through all the highs and the lows and encouraging me to pursue my interest in animal behaviour from the start.

Abstract

*Early detection of predators greatly improves prey escape and survival chances. By investigating cues left behind by predators, such as fur, urine, faeces, feathers (known as secondary predator cues, SPCs) prey may gain vital information about predators in the vicinity. This can inform defensive behaviours without the need for dangerous direct contact with a potential predator. Meerkats (*Suricata suricatta*) display an unusual mobbing-like response upon encountering SPCs, not reported in any other species. The function of this behaviour is unclear because, unlike mobbing of a live predator, this response does not yield the primary benefit of driving the threat away. An additional suggested benefit of predator mobbing is cultural transmission of information. The mobbing-like response in meerkats may function similarly in transferring information about cues associated with threats. I first investigated whether this mobbing-like response constituted a form of teaching, experimentally testing whether adults increase response intensity to promote learning in naïve pups. The results suggested that the mobbing-like response is not a form of teaching, with the presence and/or number of pups reducing response intensity. I then analysed long-term data to examine how the response to natural SPC encounters differs from predator encounters, comparing rate of animal mobbing vs mobbing-like response to SPCs. Additionally, I used the long-term data to investigate changes in behaviour (alarm calling, guarding, distance travelled and pup provisioning) in the hour before and after a SPC encounter. I also investigated the effect of pup presence on both of these responses. Again there was no evidence for teaching, with the presence and/or number of pups reducing response rate to SPCs. The presence of pups increased guarding rate generally but did not affect behavioural changes following an SPC encounter. Alarm calling rate was increased and distance travelled decreased following a SPC encounter but was not affected by the presence of pups, suggesting these are direct responses to encountering SPCs. Overall, the results suggest that the role of the mobbing-like response is not teaching, but instead functions in informing defensive group behaviour.*

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Chapter One: General introduction

Predator-prey interactions shape population dynamics and act as a key selective pressure on physiological, morphological, cognitive and behavioural phenotypes (Lima 1998). This pressure favours prey that can rapidly detect, assess and respond to predation risk, utilising visual (Sunardi *et al.* 2007; Segers & Taborsky 2012; Amo *et al.* 2017; Ayon *et al.* 2017; Billings *et al.* 2017), acoustic (Baxter *et al.* 2006; Haff & Magrath 2010; Curlis *et al.* 2016; Billings *et al.* 2017), chemical (Roth *et al.* 2008; Zöttl *et al.* 2013; Hettyey *et al.* 2015; Garvey *et al.* 2016), or kinetic cues (Warkentin 2005; Lohrey *et al.* 2009). However, while extensive research has focused on prey animals' responses to direct cues of predator presence, less attention has been paid to the use of secondary predator cues (SPCs) as indicators of predator presence in the vicinity. Secondary predator cues are cues a predator leaves behind when passing through the environment. These may include fur, urine, faeces, feathers, scent markings, regurgitation pellets, and other chemical cues. Given that the use of SPCs can aid in early detection and inform antipredator responses without the need for dangerous encounters, establishing when and how animals use such cues is central to our understanding of predator-prey interactions and their consequences.

In this introductory chapter, I begin by providing clear definitions of secondary, direct and indirect predator cues, outlining differences in their value in reducing uncertainty. I then review the literature on behavioural responses to SPCs. I highlight the transmission of social information as an important but understudied consequence of responses to SPCs and introduce key questions that will be addressed in this thesis. Finally I provide an overview of the study system used to investigate a potentially unique use of and response to SPCs.

The use of SPCs can be beneficial for prey to ascertain specific information about a potential predator without a dangerous direct interaction. Prey can use SPCs to gauge predation risk, using them to infer type of predator (Van Buskirk 2001; McGregor *et al.* 2002; Mella *et al.* 2014), predator size (Kusch *et al.* 2004), predator density and proximity (Ferrari *et al.* 2006b), predator diet (Mathis & Smith 1993; Apfelbach *et al.* 2015) and how recently the predator may have been in the area (Barnes *et al.* 2002; Zöttl *et al.* 2013; Kuijper *et al.* 2014; Van Buskirk *et al.* 2014). This information can

facilitate appropriate defensive responses in the face of a potential predator, making evasion and avoidance attempts more targeted. However, the extent to which this information helps improve survival chances has received little attention, with the majority of existing literature focusing on how and if prey process and respond to the cues. Within the literature there is also a strong taxonomic bias towards aquatic species and their responses to SPCs (see reviews, Ferrari *et al.* 2010; Mitchell *et al.* 2017), limiting our understanding of how species across taxa use these cues to inform their behaviour.

These issues are compounded by discrepancies in the nomenclature describing predator cues, which can lead to confusion and a lack of clarity in findings and interpretations of results. Cues such as urine and faeces (here described as SPCs) have been defined as being both direct (Thorson *et al.* 1998; Parsons & Blumstein 2010b; Nersesian *et al.* 2012; Zöttl *et al.* 2013) and indirect cues (Persons *et al.* 2001; Severud *et al.* 2011; Blackwell *et al.* 2018; Stryjek *et al.* 2018) by different authors. This lack of consistency in terminology could confuse matters when investigating responses to predators, conflating cases where there is a response to an actual predator with cases of responding to cues left behind. The study of responses to predator cues spans a range of fields, from evolutionary biology, neurology, conservation, behavioural ecology and chemistry; consistent nomenclature would greatly enable synthesis across disciplines. Our understanding of how animals process and use information in shaping their evolution and behaviour would be facilitated through comparable terminology in these disparate fields. In order to address these inconsistencies I propose clear definitions of direct, indirect and secondary predator cues (outlined in Table 1.1). A major distinction between these categories is the informativeness of the assessment derived from the cue of a predator's current location and threat level.

Table 1.1 – Table outlining definitions of direct, indirect and secondary predator cues.

Cue Type	Description
Direct predator cues	Direct predator cues are cues derived from the presence of a predator. These include the predator itself, as well as smells, sounds and vibrations emanating directly from the predator. Direct predator cues provide

unambiguous information about the current location, and often the type of predator through visual detection or call recognition. The sound of movement through a substrate or via vibrations also constitute a direct predator cue, providing information to pin-point predator location. They are direct indicators of a predator in close proximity.

**Indirect
predator
cues**

Indirect predator cues are cues not produced by a predator, but instead are cues associated with the possible presence of a predator. These include habitat type, the time of day, moonlight, season, conspecific alarm cues (visual, chemical or acoustic), and remains of prey that have been killed by the predator. These cues provide information about predation risk but do not originate directly from a predator, providing only a vague general indicator of current risk .

**Secondary
predator
cues**

Secondary predator cues are cues produced by a predator, although the predator does not have to be in the immediate vicinity for them to be detected. These cues may include fur, urine, faeces, feathers, scent markings, regurgitation pellets, and other chemical cues. Although SPCs do not provide a means of precisely locating a predator in the same way that direct cues do, they are more informative than indirect predator cues in terms of providing specific information about the predator.

Critically, SPCs may provide relatively safe opportunities for prey to gather information on potential threats to inform behavioural decisions. Prey can gather valuable information about a threat from SPCs, although this information may be less reliable than direct predator cues. Signal detection theory suggests that when assessing predation risk there are two types of errors possible to make; (1) responding when there is no risk (or possibly overresponding to a non-imminent threat), or (2) the more costly alternative of failing to respond to a real threat (Wiley 2006). As probability of one error decreases the other increases, however this trade-off may be overcome through inspection (Abbott & Sherratt 2013). Gathering information about a possible threat increases risk assessment accuracy, reducing likelihood of error. This may explain why inspection of SPCs is widely observed in many animals, including fish (Brown & Godin 1999), reptiles (Dial & Schwenk 1996), birds (Amo *et al.* 2011) and mammals (Belton *et al.* 2007; Furrer & Manser 2009a; Zöttl *et al.* 2013; Mella *et al.* 2014; Garvey *et al.* 2016). We may therefore consider SPC inspection as offering a

middle ground between unambiguous but dangerous assessment through direct cues and safer but vague indicators of increased risk through indirect cues. SPC inspection allows the gathering of detailed information (albeit more ambiguous) about the potential threat, reducing chance of either error.

The defensive responses upon detection of SPCs can result in plastic changes to prey morphology, physiology, reproductive and life history strategies, and behaviour. Non-behavioural responses to SPCs have been well studied, with a great deal of evidence for the hormonal changes governing non-experience dependent phenotypic changes mediated by SPCs (see reviews Ferrari *et al.* 2010; Mitchell *et al.* 2017; Parsons *et al.* 2018). For example, following exposure to corticosterone (the stress hormone) tadpoles, *Rana sylvatica*, developed larger tails, a plastic morphological change matching that observed in response to predator chemical cues and shown to improve survival (Maher *et al.* 2013). Behavioural studies primarily focus on if and what responses to SPCs are, with little understanding of the functional consequences and fitness benefits of these behaviours. The functions of certain behavioural responses are not always clear, especially in the case of seemingly predator directed defences when no predator is actually present, such as the mobbing-like responses to SPCs in meerkats, *Suricata suricatta* (Zöttl *et al.* 2013) and defensive body posturing in geckos, *Coleonyx brevis* (Dial & Schwenk 1996). In contrast to the non-behavioural responses to SPCs, it is currently unclear whether behavioural responses arise in the absence of previous experience, or are learnt either through individual experience or via social learning.

Behavioural responses to SPCs are frequently used as indicators of the ability to recognise predators using SPCs and assess whether this is learnt or requires no previous experience. Avoidance is one of the most commonly recorded responses, with studies assuming the response as indicative of experience-independent recognition and appropriate behavioural response, discounting the roles of neophobia or noxious odour repellence (Chivers *et al.* 2001; Sündermann *et al.* 2008; Apfelbach *et al.* 2015). Neophobia is an aversion to novelty, with fear of an object, location or other stimuli simply because it is novel (Greenberg & Mettke-Hofmann 2001). The assumption that avoidance responses demonstrate predator recognition rather than a reaction to a novel and/or odorous cue may lead to incorrect conclusions being drawn

about how and if SPCs inform defensive behaviours and the role of learning in the responses. Studies also use SPCs more generally in assessing what the behavioural responses are to the cues. Again, avoidance is one of the most common responses reported, yet there is no evidence supporting avoidance of SPCs aiding survival. Caution therefore needs to be taken when interpreting findings from such studies.

Behavioural responses to SPCs

Increased detection

Vigilance

One of the most common responses upon encountering SPCs is increased vigilance. This response has been observed in a multitude of species from house crickets, *Acheta domesticus* (Tanis *et al.* 2018), to domestic fowl, *Gallus gallus domesticus* (Zidar & Løvlie 2012), rabbits, *Oryctolagus cuniculus* (Monclús *et al.* 2005), stoats, *Mustela erminea* (Garvey *et al.* 2016) and meerkats (Zöttl *et al.* 2013). In wild red deer, *Cervus elaphus*, increases in vigilance continue for one week after initially encountering wolf faeces in an area (Kuijper *et al.* 2014). Heightened vigilance should aid early detection of a predator nearby, allowing prey to respond rapidly and take evasive action. If the predator is close by, the ability to visually assess the predator then provides greater information about the threat posed, informing appropriate antipredator behaviours (Amo *et al.* 2004; Lehtiniemi 2005). To date, the only experimental evidence that SPCs aids predator detection comes from a study by Zöttl *et al.* (2013), in which meerkats showed increased vigilance and more rapid detection of an experimentally presented predator model after being presented with dog urine. However, in this example, in the majority of cases (5 out of 7 trials), the individual that detected the predator was not the same individual that originally encountered the cue, suggesting that predator detection is more dependent on group rather than individual vigilance. Many of the other species responding with increased vigilance to SPCs are not group living species (e.g. stoats, rabbits and house crickets (Monclús *et al.* 2005; Garvey *et al.* 2016; Tanis *et al.* 2018)) and therefore not likely to benefit from this effect. The lack of evidence and investigation into the adaptive benefits of vigilance is surprising given that it is one of the most commonly reported behavioural responses to encountering SPCs. In particular, as increasing vigilance typically trades off against

other behaviours such as foraging, understanding how responses to SPCs may promote fitness is a clear priority for future research.

Detection methods

After initially encountering a SPC, prey may not only increase vigilance, but invest in other behaviours which assist in detecting predators. Wall lizards, *Podarcis muralis*, for example, increase tongue flicking rate and reduce latency to first tongue flick in response to predatory snake scent (Amo *et al.* 2004). This change in tongue flicking behaviour allows the lizards to quickly gather information regarding the source of the scent. Their main predator, the smooth snake, *Coronella austriaca*, shares the same habitat as the lizards, occupying the same refuge crevices. Use of chemical cues therefore allows the lizard to assess risk before entering the crevice where visual cues are limited. Another detection method employed by some animals after encountering SPCs is sniffing the air (Caine & Weldon 1989; Terlouw *et al.* 1998). Sniffing the air may provide information about which direction the predator may be, allowing them to move away from the source of the threat. The initial encounter of an SPC leads to the use of further detection methods to accurately assess current risk. However, again there is no evidence, as yet, that this information gathering improves prey survival chances.

Reducing non-defensive behaviours

Reduction in foraging

Reduction in foraging activity is another common response to detecting SPCs (Berejikian *et al.* 2003; Sike & Rózsa 2006; Roth *et al.* 2008; Parsons & Blumstein 2010a; Nersesian *et al.* 2012). The reduction in foraging activity is unlikely to be an adaptive response *per se* but rather the result of a trade-off against increased investment in other antipredator behaviours such as vigilance, moving away, taking refuge, reduced overall activity and cue inspection or mobbing. Indeed, reductions in foraging are often related to increases in vigilance (Brinkerhoff *et al.* 2005; Zidar & Løvlie 2012; Tanis *et al.* 2018), and to an avoidance of feeding in areas containing the cue (Grostal & Dicke 1999; Shrader *et al.* 2008; Weiss *et al.* 2015). SPCs can be indicative of predation risk in an area, so either increasing vigilance or preferentially foraging in areas of lower risk is adaptive. In particular, for some animals, they are

especially vulnerable to predation whilst feeding as their vision is compromised with their heads down (Krause & Godin 1996). This trade-off between foraging and antipredator behaviours is why rapid, accurate assessment of risk is so valuable, in order to only respond when actually necessary.

Reduction in parental care

Detection of SPCs can also alter parental care behaviour, reducing investment in offspring. For example, in response to ferret scent, blue tits, *Cyanistes caeruleus*, reduced time spent in the nest box and on non-essential activities, to reduce risk of predation to themselves (Amo *et al.* 2017). Nevertheless, offspring did not appear to suffer as a result of this as provisioning rate remained unchanged. In mice, mothers reduced maternal care, in the form of licking of offspring, as a stress response to bobcat urine (St-Cyr & McGowan 2015). Whether this change in behaviour has any functional benefit is unclear: it may be there is a trade-off between maternal care and other behaviours such as vigilance, or it could be the result of a pathological response to stress. The use of SPCs to inform behaviour related to parental care suggests that these cues provide valuable information about current threat levels, particularly as investment in offspring is an integral part of parental fitness.

Reduction in scent marking

Reduction in scent marking by prey species has been reported in response to SPC encounters. This could both reduce time on a non-defensive behaviour and reduce chance of detection by predators. Wild male Eurasian beavers, *Castor fiber*, and male laboratory mice, *Mus musculus*, reduce territorial scent marking in response to an intruders scent when a predator scent was also present (Roberts 2001; Rosell & Sanda 2006). Both studies also found that males reduced marking when a novel non-predator scent was present, although the response to predator treatments was greater. These studies indicate that a neophobic response to a novel scent is enough to induce a significant behavioural change, albeit to a lesser degree than in response to a predator scent. These findings highlight the importance of presenting a novel non-threatening stimulus as well as a predator cue to determine whether the response is neophobia specific response to predator cues, or a more general manifestation of neophobia. The reduction in scent marking shown seems to be a defensive response to encountering a SPC. Scent marking can advertise an individual's location, which is

beneficial in conspecific communication for mating and territorial defence, but costly if intercepted by a predator. Survival rate of various vole species is lowered in plots treated with scent marks than untreated controls (Koivula & Korpimäki 2001). To our knowledge there is no evidence for predators reducing their scent markings in order to facilitate more successful hunting, however if SPCs are important cues in predator detection and avoidance this would be an interesting avenue to explore.

Predator evasion

Reducing activity

Many species across taxa reduce activity in response to SPCs. Decreased activity may reduce probability of being detected or encountered by predator and conserves energy which may be needed to mount an escape, potentially aiding survival. Many species employ this tactic, including wolf spiders, *Pardosa milvina* (Persons *et al.* 2001), stickleback larvae, *Gasterosteus aculeatus* (Lehtiniemi 2005), red-backed salamanders, *Plethodon cinereus* (Sullivan *et al.* 2002) and mice (St-Cyr & McGowan 2015). Various predators use movement to detect their prey (Persons & Uetz 1997; Catania *et al.* 2008; Miyai *et al.* 2016), so freezing or reducing movement reduces likelihood of being detected. The effectiveness of reduction in activity as an antipredator behaviour is one of the few adaptive benefits to have been examined in the literature. In prey wolf spiders, those that increased immobility and slowed movement in response to predator cues had enhanced survival when paired with the live predator (Persons *et al.* 2001). Common garden skinks, *Lampropholis guichenoti*, were also less active and mobile in response to predator cues (Downes 2002). This reduction in activity decreased the likelihood of being detected by the live predator; once an individual was detected this almost always lead to capture.

Avoidance

Avoidance of the immediate area where an SPC is encountered is perhaps the most widespread and commonly reported response (Caine & Weldon 1989; Grostal & Dicke 1999; Sike & Rózsa 2006; Roth *et al.* 2008; Amo *et al.* 2011; Severud *et al.* 2011; Apfelbach *et al.* 2015; Weiss *et al.* 2015). It is also the aspect of the field where interpretation of the results is most problematic. Many studies report avoidance responses to SPCs and state that these are indicative of both predator recognition and

an appropriate behavioural response. These studies are often on captive animals where avoidance of a specific area or resource has few or no negative consequences (Masini *et al.* 2005; Monclús *et al.* 2005; Kobayakawa *et al.* 2007), or in studies without a novel, odorous control, making difficult to determine whether avoidance is predator related, pungent odour avoidance, or a neophobic response to a novel cue (Chivers *et al.* 2001; Sündermann *et al.* 2008; Apfelbach *et al.* 2015). Neophobia, or fear of novelty, is often an adaptive defensive response in avoiding novel, potentially dangerous stimuli (Greenberg & Mettke-Hofmann 2001; Greggor *et al.* 2015). There is evidence for odour neophobia in Trinidadian guppies, *Poecilia reticulata*, and whitetail damselfish, *Pomacentrus chrysurus* (Brown *et al.* 2013; Ferrari *et al.* 2018). Many studies use a so called novel-odour, such as perfume (Amo *et al.* 2004, 2011; Weiss *et al.* 2015) or cinnamon (Garvey *et al.* 2016), in an attempt to control for a neophobic response. Although these odours may be pungent to humans they may not be equally salient to the study species, so careful selection of suitable biologically relevant stimuli is critical (Greggor *et al.* 2015). The scarcity of studies using a pungent novel odour makes it difficult to distinguish the basis of cue avoidance. An avoidance response is generally associated with a trade-off, because avoiding an area may generate costs such as lost foraging and mating opportunities, and possibly loss of a territory. Avoidance of SPCs, whether as a result of neophobia or predator recognition, may still be an adaptive response, but caution needs to be taken when interpreting these results as representative of predator-specific recognition. Moreover, it is important to note that there is currently no evidence to support SPC avoidance enhancing survival.

Movement

One seemingly simple way to avoid encountering a predator is to move away from an area in which an SPC was detected, rather than just avoiding the immediate vicinity of the cue. This can be via fleeing from the cue (Amo *et al.* 2004; Mella *et al.* 2014) or altering space use, such as shifting foraging to perceived safe areas (Brinkerhoff *et al.* 2005; Shrader *et al.* 2008), and changing trail use (Severud *et al.* 2011). Use of SPCs in this way may be more common in areas where predation risk is heterogeneous, such as in areas with territorial predators (Ward *et al.* 1997; Eichholz *et al.* 2012), as SPCs are likely to be accurate indicators of predator space use and likelihood of encounter. This is in line with the “ecology of fear” literature, which suggests that prey

use perceived predation risk throughout their territory to inform their space use, utilising information from using SPC presence and other direct and indirect predator cues (Brown *et al.* 1999; Laundré *et al.* 2010). In this way prey move out of areas of high risk into areas of low risk in order to minimise risk of predation; this is only possible if predation risk is heterogenous. In group-living species, detection of SPCs may act in improving group cohesion, reducing distance between individuals and coordinating movement away from the cue. For instance, freshwater amphipods, *Gammarus pulex*, and common toad tadpoles, *Bufo bufo*, increase aggregation in response to predator odours (Watt *et al.* 1997; Kullmann *et al.* 2008). However, there may be risks associated with using SPCs as a cue to move away, because cues will not necessarily be informative about the predator's direction of travel. Responses to ambiguous cues could therefore inadvertently lead to animals moving closer to the potential danger.

Refuge use

Another way in which animals reduce their risk of being detected and evade predation is by taking refuge. These refuges can be in the form of burrows, crevices, vegetation or any form of shelter. Utilising refuges reduces the likelihood of being detected by a predator thereby increasing chance of survival. However there is no evidence to support this as an adaptive response to SPCs. Individuals spend longer in refuges after encountering SPCs (McGregor *et al.* 2002; Sullivan *et al.* 2002; Ferrari *et al.* 2006a; Belton *et al.* 2007), and in the case of pike, *Esox lucius*, and stickleback larvae, the vegetation refuge taken in the face of SPCs was otherwise avoided as it reduces foraging ability (Lehtiniemi 2005). This illustrates the trade-off associated with refuge use, as generally hiding reduces ability to forage and likely other activities such as finding mates.

Changing nesting behaviour

Another potential way to evade predation is through changes in nesting behaviour in response to SPCs. Spider mites, *Tetranychus urticae*, for example, avoid ovipositioning on leaves treated with predatory mite cues (Grostal & Dicke 1999), while great tits, *Parus major*, and other cavity nesting birds were more likely to choose nest boxes without predator cues (Ekner & Tryjanowski 2008; Amo *et al.* 2011). Similarly, dabbling ducks reduced nesting on predator urine-treated plots (Eichholz *et al.* 2012). This use of SPCs was suggested to be a learnt association between SPCs and

increased predation risk, as some individuals continued to nest on urine treated plots indicating they may not have learnt the risks associated with the cues. The information gained from SPCs allows animals to lay in “safe” areas. If the cues are representative of increased predation risk, then this behaviour is adaptive by choosing not to lay at risky sites. However, if the cues are not representative of a true risk then this may result in laying on suboptimal sites and wasting time and energy locating a new site. Using SPCs in this context may allow for a greater degree of certainty about the type of threat than indirect cues, but not require a dangerous predator encounter for this information to be gained. So far there is no evidence to suggest that offspring survival is enhanced by altering nesting behaviour in response to SPCs.

Deterrence behaviours

Predator deterrence

Some animals display predator deterrence behaviours in response to SPCs. Animals such as Siberian chipmunks, *Eutamias sibiricus* (Kobayashi 2000) rock squirrels, *Otospermophilus variegatus*, and Californian ground squirrels, *Otospermophilus beecheyi* (Clucas *et al.* 2008b) engage in snake scent-application behaviour. This involves chewing on snake skin and applying it to their body. This is thought to be a form of anti-predator behaviour, masking an individual’s scent with that of a snake. In support of this, rattlesnakes were found to spend less time and fewer tongue flicks when investigating squirrel and rattlesnake scent combined compared to squirrel scent alone (Clucas *et al.* 2008a). Common waxbills, *Estrilda astrild*, also appear to use SPCs as a predator deterrent, by incorporating predator scat into their nests (Schuetz 2005). This may act either as an olfactory deterrent or serve as an olfactory camouflage for the nest against potential predators. Nests treated with predator scat suffered less predation than untreated control nests, indicating a clear fitness benefit as a result of this behaviour. Geckos after exposure to snake skin chemicals perform a defensive tail display, raising their tail in the direction of the predator in an arch over the body and moving it side to side (Dial & Schwenk 1996). This behaviour is suggested to both signal to the predator that it has been spotted, and to entice the predator to attack the tail (rather than the body), facilitating escape, although in this context there was no predator present. The function of this seemingly predator directed behaviour in a situation where there is not a predator is unclear. One,

possibility is that it is an inflexible, reflexive response to encountering any cue of predation, or that it is uncommon for this species to detect predator chemical cues when a predator is not in close proximity.

Gathering information

Inspection and recruitment

Inspection of SPCs is thought to provide a relatively safe opportunity to gather more information about the threat. Gathering information about a possible threat increases risk assessment accuracy, reducing likelihood of an erroneous response. This may explain why inspection of SPCs is widely observed in many animals, including fish (Brown & Godin 1999), birds (Amo *et al.* 2011) and mammals (Belton *et al.* 2007; Furrer & Manser 2009a; Zöttl *et al.* 2013; Mella *et al.* 2014; Garvey *et al.* 2016). Through inspection, prey can assess the risk posed and initiate the most appropriate behavioural response, be it heightened vigilance, fleeing or seeking refuge. Many mammals display inspection behaviour of SPCs followed by increased vigilance (Belton *et al.* 2007; Furrer & Manser 2009a; Zöttl *et al.* 2013; Mella *et al.* 2014; Garvey *et al.* 2016). The subsequent vigilance following inspection may function in determining whether the threat is still nearby, and for individuals to be on alert for possible attack. Inspection behaviour typically involves cautious approach to the cue, sniffing and visually assessing it. In some cases individuals will recruit other group members to investigate the cue through recruitment calls (Furrer & Manser 2009a; Zöttl *et al.* 2013; Collier *et al.* 2017). This recruitment behaviour is thought to act in alerting other group members to the apparent risk in the area and increase vigilance. Meerkats take this recruitment response one step further, by not only recruiting individuals to the cue but also displaying a mobbing-like response.

The unusual mobbing-like response of SPCs in meerkats forms the central focus of this thesis. Typical mobbing of a live predator involves the gathering of individuals around a threat, with individuals approaching the source of the threat, investigating it, making easily localizable calls, and characteristic display behaviours (Curio *et al.* 1978b; Graw & Manser 2007; Randler & Vollmer 2013). The mobbing-like response towards SPCs, to our knowledge only documented in meerkats (Graw & Manser 2007; Zöttl *et al.* 2013), closely resembles the response shown upon encountering an actual

predator. The function of mobbing-like response to SPCs is not understood. The primary function of mobbing is thought to be predator deterrence (Curio *et al.* 1978b; Graw & Manser 2007), yet given this response to SPCs is unlikely to deter a predator as the predator is not present, there must be some alternative function. One possibility is that mobbing-like response may be a way to increase group vigilance and chance of detecting a threat, improving group cohesion in moving away from the potentially unsafe area, or simply a by-product of arousal. Another, as yet unexplored possibility is that overt mobbing-like response to SPCs, could serve as a form of teaching for naïve young to learn about predator characteristics and how to respond.

Role of learning in SPC recognition and responses

Whether or not recognition and responses to SPCs are learnt is not entirely clear. In many instances naïve prey have been shown to display aversive responses, such as avoidance, to SPCs (Punzo 2007; Amo *et al.* 2011; Weiss *et al.* 2015). For example, predator-naïve dwarf hamsters inspect and avoid ferret urine, discriminating and showing greater avoidance towards urine from hamster-fed ferrets than mice-fed (Apfelbach *et al.* 2015). This suggests that independent of experience, individuals are able to recognise and respond to cues representative of a greater threat. However, caution needs to be taken when using avoidance in this way, not to confuse neophobia with non-learnt predator recognition. Great tits showed greater avoidance of novel control cologne than mustelid scent markings (Amo *et al.* 2011). Experience-independent SPC recognition is not ubiquitous. Work on tammar wallabies, *Macropus eugenii*, demonstrated that predator-naïve individuals do not respond to SPCs whereas predator-experienced individuals do, suggesting that there is a role for learning in responding appropriately to SPCs (Blumstein *et al.* 2002). It may be that general responses to risk require no prior experience and are brought about through fear/stress responses to certain or novel stimuli, while the more dynamic, predator-specific or risk-dependent responses to threats may need to be learnt via personal experience or social learning.

The necessity for learning about SPCs may be more common under certain conditions. When predation risk varies a generalised response may not be appropriate and a tailored response to the threat posed may be more adaptive. Constant learning

may be necessary in adjusting responses to reflect current risk. Threat-sensitive responses allow individuals to respond with a suitable degree of severity, preventing over-responding and therefore time and energy wasted. Variation in risk may be driven by prey being at risk from multiple predators with different hunting strategies and/or sensory modalities, or when predation risk varies spatially or temporally. For example, stoats responded to both sympatric (cats and ferrets) and novel predator (African wild dog) cues by inspecting the cues and increasing vigilance (a generalised response). However, the stoats had more pronounced behavioural changes in response to the sympatric predators (Garvey et al. 2016). The behavioural responses differed between the two sympatric species, although stoats had an overall stronger response to ferret cues, they showed greater scanning behaviour to cats which pose above ground than ferrets. This suggests that stoats may learn the most appropriate defensive responses for different predators.

Interacting with and inspecting SPCs may provide an important learning opportunity to recognise cues associated with risk. As highlighted above, inspection is a common response and allows individuals to gather more detailed information about the cue. For prey to learn predator-specific responses requires the ability to distinguish between certain predator characteristics and associate them with appropriate defensive responses. SPCs may offer a unique way to do this through the learning of predator characteristics and the risk associated without direct contact. For example, naïve glowlight tetras, *Hemigrammus erythrozonus*, learn to visually recognise their cichlid predators after exposure and inspection of predator odour containing conspecific alarm pheromones (Brown & Godin 1999). Only inspectors acquired visual recognition of the predator and display antipredator behaviours. Cue inspection facilitated tetras to learn olfactory predator characteristics and associate them with the live threat. Information from conspecific alarm pheromones paired with SPCs offers an opportunity for social learning (Griffin 2004). Rainbow trout, *Oncorhynchus mykiss*, are able to learn predator recognition through a single conditioning event of predator odour and conspecific alarm cues (Brown et al. 2011). The role of social learning in relation to SPCs, outside of the use of conspecific cues, has received little attention. To our knowledge, there is no evidence of social learning via SPCs in terrestrial animals. However, this does not mean social learning is not taking place. Naïve individuals may learn how to recognise and respond to SPCs through the observation

of conspecifics responses to the cues. Due to the high risk nature of learning about predators it may be beneficial for knowledgeable individuals to facilitate rapid learning about threats.

The mobbing-like response towards SPCs observed in meerkats may provide an opportunity for social learning, and more specifically may constitute a form of teaching. Teaching is an active form of social learning which involves knowledgeable individuals modifying their behaviour so as to promote learning in others (Caro & Hauser 1992; Thornton & Raihani 2008). One of the proposed functions for the mobbing of live predators is the cultural transmission of threat recognition (Curio *et al.* 1978a), with evidence that Siberian jays, *Perisoreus infaustus*, may learn to recognise and respond to predators after observing a single mobbing event and have enhanced survival as a result (Griesser & Suzuki 2017). Conspicuous mobbing-like responses towards SPCs by adults in the presence of naïve young could potentially act as a form of “opportunity teaching” (Caro & Hauser 1992), providing young with a relatively safe environment in which to learn the cues associated with a threat and how to respond appropriately. While this possibility has never been tested, learning has been indicated to play an important role in responding to SPCs (Blumstein *et al.* 2002) and can be facilitated by social learning (Brown & Godin 1999; Ferrari *et al.* 2006a; Mirza *et al.* 2006; Brown *et al.* 2011; Crane *et al.* 2015). Following Caro & Hauser’s (1992) operational criteria, the mobbing-like response to SPCs would constitute a form of teaching if (1) adults would modify their behaviour in the presence of naïve pups – for instance by responding to the cues more intensely, (2) adults incur a cost or no immediate benefit from this but (3) pups learn to recognise and respond appropriately to SPCs as a result of exposure to adult mobbing.

In this thesis I use a combination of experiments and long-term behavioural data to test whether adult meerkats modify their mobbing-like response intensity to promote learning in the presence of naïve pups. In Chapter two, I use experimental presentations of SPCs to test whether and how adults respond to SPCs with and without the presence of pups, and whether response intensity varies depending on the novelty of the cue. In Chapter three, I then use long-term data to investigate how the mobbing-like response varies from the mobbing of an actual predator, by examining the response rate of natural predator and SPC encounters. I also use this long-term

data to determine whether there are behavioural changes (alarm calling, guarding, distance travelled and pup provisioning) following an SPC encounter and how these may vary with the presence of pups and abiotic constraints (Chapter three). I use these results to test whether meerkats use information derived from investigating SPCs in informing subsequent group defensive behaviours, such as vigilance and group cohesion.

Study system

Meerkats offer a fascinating opportunity to investigate a seemingly unique behaviour in the mobbing-like response to SPCs. Meerkats are a species of cooperatively breeding mongoose found in the semi-arid regions of South-Western Africa (Clutton-Brock & Manser 2016). They live in social groups ranging from 3-47, averaging 15 individuals (Clutton-Brock & Manser 2016; Wyman *et al.* 2017). Breeding is generally monopolised by a dominant pair and subordinate helpers contribute to the care of offspring and other group defensive behaviours. Pups are dependent on provisioning until 3 months old, giving them ample opportunity to observe and learn from other group members, including foraging skills and conspecific alarm calls (Hollén & Manser 2006; Thornton & McAuliffe 2006; Hollén *et al.* 2008). Meerkats forage as a cohesive group and often have an acting sentinel undertaking vigilance for the group allowing the rest of the group to focus on foraging (Santema & Clutton-Brock 2013; Rauber & Manser 2017). Referential alarm calls are used to distinguish urgency (high or low) for terrestrial or aerial predators and recruitment (Manser 2001; Manser *et al.* 2001).

All data collection was conducted at the Kalahari Meerkat Project in and around the Kuruman River Reserve, South Africa (Clutton-Brock *et al.* 1998). For the past 20 years this population has been monitored as part of on-going research on a whole host of aspects of the meerkats' behaviour, ecology and life history (Clutton-Brock & Manser 2016). This long-term monitoring provides a wealth of data with a population of individually identifiable animals, the majority of which have been followed from birth, and regular behaviour and condition data collected. All individuals are habituated to observation at < 1m, allowing for both the long-term behavioural observations and my experimental predator cue presentations. Experimental cue presentations were conducted on six groups ranging from 3-24 individuals over the breeding season from October 2017 to May 2018. For analysis of the long-term data I analysed records from 11/04/1999 (the first recorded SPC recruitment event) to 30/04/2019.

Chapter Two: Mobbing-like response to secondary predator cues is not a form of teaching in meerkats

*Across many taxa, individuals learn how to detect, recognise and respond to predators via social learning. Learning to recognise and interpret predator cues is essential in the accurate assessment of risk. Cues can come directly from a predator's presence (visual, acoustic) or from secondary predator cues (SPCs, such as hair/feathers, urine, faeces, etc.) left in the environment. Animals show various responses to encountering SPCs, which are thought to act in reducing risk to the individual. Meerkats, *Suricata suricatta*, show a response to SPCs not described in any other species: they display a mobbing-like behaviour. The function of this behaviour is unclear as unlike mobbing, the response it so closely resembles, it cannot serve to drive predators away. I used experiments to investigate whether one aspect of this mobbing-like response acts in teaching naïve young how to recognise and respond to predators. I tested whether wild adult meerkats respond more intensely to SPCs in the presence of naïve pups to promote learning. Meerkats are one of a handful of species that have been shown to teach. If the mobbing-like response to SPCs was shown to be a form of teaching this would provide the first evidence of teaching in multiple contexts outside of humans. I presented SPCs to adults with and without pups present. If the mobbing-like response to SPCs serves to promote learning, adults' response intensity should increase when pups are present. Contrary to this prediction, response intensity declined when pups were present, possibly due to costs associated with foraging with pups. Group size and cue type presented also influenced response intensity. These results suggest that the mobbing-like response to SPCs is not a form of teaching in meerkats. Instead, this behaviour may function in information transfer to others. Exposing group members to SPCs may better inform them of the nature of the threat, facilitating more effective defensive responses.*

Introduction

The ability to mount appropriate defensive behaviours in the face of predation is vital to prey survival. Accurately assessing current predation risk aids in informing risk-appropriate behaviours, limiting unnecessary time and energy expenditure on non-acute or non-immediate threats. Individuals can gauge predation risk through personal assessment of the current situation and from the risk assessments of others, by using social information (Dall *et al.* 2005; Crane & Ferrari 2013). Access to social information has been shown to be a key benefit of group living, aiding in detecting, recognising and responding appropriately to predators. Social learning about predators is widespread across taxa (see reviews: Griffin 2004; Crane & Ferrari 2013). Mobbing is a common antipredator behavioural response often learnt via social learning (Curio *et al.* 1978a; Davies & Welbergen 2009; Cornell *et al.* 2012; Feeney & Langmore 2013; Griesser & Suzuki 2017).

Mobbing is a method of predator deterrence which involves the gathering of individuals around a potential threat, with individuals approaching the threat, investigating and uttering calls (Curio *et al.* 1978b; Graw & Manser 2007). Mobbing is conspicuous and costly in terms of time and energy expenditure, advertises an individual's location, and increases risk of injury or mortality to the individual (Curio *et al.* 1978b; Krama & Krams 2005; Tórréz *et al.* 2012). Although mobbing is costly it also provides important advantages. Mobbing may offer ample opportunities for individuals to learn to recognise and respond appropriately towards predators by observing conspecifics' behaviour. Naïve juvenile Siberian jays, *Perisoreus infaustus*, learnt to both recognise and mob a predatory goshawk, *Accipiter gentilis*, following a single observation of a knowledgeable individual mobbing the predator (Griesser & Suzuki 2017). However the principal benefit of mobbing is thought to be predator deterrence, driving away a predator. This is through either intimidation of the predator, or alerting it that it has been detected thus reducing the chance of successful attack (Caro 2005; Abolins-Abols & Ketterson 2017). While the benefits of mobbing and driving a predator away are clear, the benefits of the peculiar mobbing-like response of secondary predator cues (SPCs) observed in meerkats, *Suricata suricatta*, are less apparent as this does not act in driving the threat away.

Secondary predator cues are cues left in the environment by predators; such as fur, urine, faeces, feathers, scent markings and regurgitation pellets. These cues can indicate predator presence in the vicinity and provide information about the nature of the threat. In most cases prey avoid SPCs often responding with defensive behaviours such as increased vigilance (Monclús *et al.* 2005; Zidar & Løvlie 2012; Garvey *et al.* 2016; Tanis *et al.* 2018), reduced activity (Persons *et al.* 2001; Sullivan *et al.* 2002; Lehtiniemi 2005), refuge use (McGregor *et al.* 2002; Sullivan *et al.* 2002; Ferrari *et al.* 2006a; Belton *et al.* 2007), and moving away from the cue (Amo *et al.* 2004; Shrader *et al.* 2008; Mella *et al.* 2014). However, some species respond by approaching these cues. Individuals approach the cues in order to inspect them to gain further information about the source of the cue (Belton *et al.* 2007; Furrer & Manser 2009a; Zöttl *et al.* 2013; Garvey *et al.* 2016; Collier *et al.* 2017). Some species are able to ascertain the type of predator (Van Buskirk 2001; McGregor *et al.* 2002; Mella *et al.* 2014), predator size (Kusch *et al.* 2004), age of the cue (Barnes *et al.* 2002; Zöttl *et al.* 2013; Kuijper *et al.* 2014) and the predator's diet from these cues (Mathis & Smith 1993; Apfelbach *et al.* 2015). Meerkats take this inspection behaviour one step further by responding in a mobbing-like way to SPCs while investigating them, and to our knowledge are the only species to respond in this way. When meerkats encounter SPCs they approach and investigate the cues, raising their tails, piloerecting (raising their fur) and making recruitment calls. The mobbing-like response to SPCs is without the inherent benefit of the behaviour it so closely resembles: deterring a predator. There is no clear benefit of responding to a non-threatening SPC as if encountering the threat itself, particularly as the response is costly in time and energy and also conspicuous. One potential aspect of a mobbing-like response towards SPCs by meerkats is that it is a form of teaching.

Teaching is a form of active social learning. According to established criteria, teaching involves (i) an individual, A, modifies its behaviour in the presence of a naïve observer, B, (ii) A incurs a cost or no immediate benefit by doing so, (iii) as a result of A's behaviour B acquires a skill or knowledge faster than it would have otherwise, if at all (Caro & Hauser 1992). Teaching was previously regarded as uniquely humans, but there is growing evidence that non-human animals across taxa also teach. Meerkats are one of only a handful of species shown to teach (Thornton & McAuliffe 2006), alongside tandem running ants, *Temnothorax albipennis* (Franks & Richardson 2006)

and some species of birds (Raihani & Ridley 2008; Kleindorfer *et al.* 2014; Chen *et al.* 2016).

If the mobbing-like response to SPCs is in part a form of teaching then this would provide the first evidence for teaching in multiple contexts outside of humans. Passive social learning may be sufficient to learn about SPCs through group recruitment events. However, the unusual mobbing-like response in meerkats may suggest there is an additional aspect of this behaviour in actively inciting other group members to inspect the cue. This behaviour may act in transferring information and promoting learning in naïve individuals. Inspecting and responding to SPCs in the presence of pups may provide a safe environment for naïve pups to learn predator characteristics and the appropriate behavioural responses. During an SPC encounter naïve pups are able to obtain information on the odour characteristics of predators and how to respond, without dangerous exposure to the predator itself. Adults may exaggerate their response to cues to promote learning in pups, using a high arousal signal to attract pups and displaying an appropriate response to a threat. Given that meerkats do recruit to and inspect SPCs without the presence of pups, the key aspect to investigate is whether the intensity of the mobbing-like response increases when pups are foraging with the group. If adults do modify their behaviour and increase response intensity in the presence of pups, then the mobbing-like response to SPCs may constitute a form of teaching. Active teaching, rather than more passive social learning, may be occurring in this context as it provides an optimal learning environment for naïve pups to rapidly learn essential predator recognition and response enhanced by adults' behaviour. Alternative explanations for this unusual behaviour, not explored as part of this study, may be that the mobbing-like response acts in alerting and informing group members of possible predator presence to increase group vigilance and aid detection, to improve group cohesion, or simply a by-product of arousal.

Meerkats are a cooperatively breeding mongoose species from the arid regions of southern Africa, in which all group members contribute to the raising of young (for more detailed information see: Clutton-Brock & Manser 2016). Pups (aged 0-3 months) are heavily reliant on group members for care, protection and resources. This dependence gives pups abundant opportunity to learn knowledge and skills from other

group members as they follow them around begging for food. One such example is learning how to handle dangerous prey items, such as scorpions. Adults teach pups how to safely and effectively handle scorpions by initially provisioning them with dead or modified individuals (claws and/or sting removed) gradually providing pups more intact and alive prey as they get older (Thornton & McAuliffe 2006). Meerkat pups not only use social information in acquiring foraging skills but also in developing and honing anti-predator responses. Younger pups typically respond to alarm calls by running to the nearest adult, and alarm call more often at non-threatening stimuli, with their responses becoming more adult-like as they age (Hollén & Manser 2006; Hollén *et al.* 2008). The development of appropriate responses to alarm calls appears to be experience-dependent and likely a result of social learning. These examples highlight the importance of social learning and teaching in meerkats pups' behavioural development and provide the foundations for the possible function of the mobbing-like response to SPCs being teaching.

This study uses experimental presentations to investigate the function of the mobbing-like response to SPCs in wild meerkats. Specifically, I test whether such a response may constitute a form of teaching, with adults modifying their behaviour so as to promote learning in pups. Meerkats commonly respond to both predators and SPCs by approaching, making recruitment calls, raising their tails and piloerecting their fur (Graw & Manser 2007). I predicted that, as per the first criterion of Caro and Hauser's definition of teaching (Caro & Hauser 1992) the intensity of these responses would be greater when pups were present and when cues were novel to the pups but not adults.

Methods

Study site & species

Experiments were carried out on 6 groups of wild meerkats at the Kalahari Meerkat Project in and around the Kuruman River Reserve, South Africa (Clutton-Brock *et al.* 1998). All members of the population used in the experiments were habituated to observations at < 1 m, with individuals identifiable from unique dye marks on their backs (Jordan *et al.* 2007). Group sizes ranged from 3-24 and the life history of all group members were known as part of long-term study of the population for over 20 years.

Cues

I used two different cue types: (1) domestic cat, *Felis catus*, urine samples, obtained from local veterinary surgeries during medical procedures and stored in the freezer and (2) African wildcat, *Felis lybica*, fur samples, obtained from a recently deceased individual found (within 6 hours of death) on the reserve and stored in the freezer. Both domestic cats and wildcats are common predators on the reserve. Adults are likely to have encountered the predators and their associated cues previously but it is highly likely that pups are naïve. Pilot studies determined that adults responded to both predator cues with a mobbing response. Samples were portioned into 5 mls of urine and 0.1 g of fur and stored at -20 °C. To ensure that meerkats were responding specifically to the cues and not the experimental set-up, equivalent quantities of water and dry grass were used as matched controls for the urine and fur respectively. To simplify methodology cues from non-predatory controls were not used after previous work showed little response by meerkats to ungulate control cues, indicating that responses to predator cues are not due to cue novelty or general investigation but recognition of predator cues (Zöttl *et al.* 2013). Cues were defrosted shortly before use in a presentation. Latex gloves were worn when handling the cues to prevent contamination with human scent.

Presentations

Presentations were carried out while the group were foraging in the morning. The first trial at a group was after the birth of pups but while pups were still being babysat at

the burrow, and had not begun foraging with the group (no pups: NP). This allowed conditions to be kept as similar as possible across trials (including hormonal changes associated with reproductive events), while still allowing comparison of trials with and without pups. Pups began foraging with the group at around three-four weeks of age, but initially spent much of their time in sheltered locations (e.g. in boltholes or under bushes) begging for food and did not participate in group alarm or mobbing events. The second trial, with pups present (pups present 1: PP1) was conducted when pups were approximately six-seven weeks (21 ± 3 days after they began foraging with the group) and spent the majority of the time actively moving between helpers. Subsequent trials (pups present 2 and 3: PP2 and PP3) were conducted at one week (7 ± 1 day) intervals. For trials 1-3 (NP, PP1, PP2) the same cue type was used and for trial 4 (PP3) a different cue was used, representing a novel cue (Table 2.1). I predicted that adults would show the lowest mobbing intensity to PP2 as the cue type was not novel to pups or adults. Half of the groups were presented one combination of cues (Group A – urine, urine, urine, fur) and the other were presented the opposite (Group B – fur, fur, fur, urine). For each trial a cue was presented and a control, with a randomised order of predator or control presentation. The second cue was presented ten minutes after the interaction with the initial presentation had ended.

Table 2.1. – Table of the four experimental trials showing the conditions, cue type, cue novelty, pup age and pup location.

	Trial 1 - NP		Trial 2 - PP1		Trial 3 - PP2		Trial 4 - PP3	
Treatment	No pups		Pups present 1		Pups present 2		Pups present 3	
Cue	A. Urine	B. Fur	A. Urine	B. Fur	A. Urine	B. Fur	A. Fur	B. Urine
Cue novelty?	Yes – to adults		Yes – to pups		No		Yes – to adults & pups	
Pup age	<i>24 days \pm 3 days</i>		<i>49 days \pm 3 days</i>		<i>56 days \pm 3 days</i>		<i>63 days \pm 3 days</i>	
Pups foraging?	<i>Pups babysat at burrow</i>		<i>Foraging with group for 21 days</i>		<i>Foraging with group for 28 days</i>		<i>Foraging with group for 35 days</i>	

Cues were presented 30 minutes after the group had left the burrow in the morning to begin foraging, and after 10 minutes of normal foraging behaviour following an alarm event, so as to minimise the effect of any previous stress on responses to the presentation. The cues were presented in a petri dish filled with sand at the end of a

1 m pole, to reduce association of cues with the human presenter. One week prior to beginning the experimental presentations the cue presentation apparatus was presented to all group members filled only with sand to habituate them to the set up and ensure that responses during the experimental trials were to the cue and not the apparatus. The experimental presentations were to a randomly selected focal individual (non-pup) from the group. If an individual did not initially respond to the cue it was presented again up to three times. If this still did not elicit a response the cue was presented to another randomly chosen individual to prevent over exposure to the cue to any one individual. A trial began once an individual responded to and began interacting with the cue. Trials were conducted at least one week apart to reduce possible habituation to the cues. Presentations were video recorded using a GoPro (Hero 4) and audio recorded using a microphone (Sennheiser ME 66 with a K6 powering module) connected to a recorder (Marantz Solid State Recorder PMD661 MKII) at a distance of approximately 1-1.5m from the cue presentation.

Behavioural analysis

Video recordings were coded using BORIS (Friard & Gamba 2016), noting the behaviours of each individual that interacted with the cue. Details and definitions of the behaviours recorded are given in Table 2.2. It was only possible to identify and record the behaviours of each individual if they were within 5m of the cue presentation, due to video quality and vegetation. Only the behaviours of individuals that interacted with the cues were recorded. Presentations to non-responding target individuals were not included in the analysis if a subsequent presentation to another group member elicited a response.

Table 2.2. – Ethogram of the behaviours analysed in response to the secondary predator cue presentations.

Behaviour	Description
Interact	<i>Duration of time spent interacting with the cue, when the individual was within 0.3 m of the cue (indicating a direct interaction). From when they first approached the cue until they left. Behaviours included facing the cue directly, touching and sniffing the cue, rocking back and forth facing the cue. Interaction ended when an individual was quadrupedally vigilant (scanning on four legs), on bipedal vigilance (scanning on two</i>

	<i>legs), or resumed foraging. New interaction began if they started interacting again.</i>
Tail raise	<i>Tail raised vertically above their body within 0.5 m of the cue (within close proximity). Recorded the duration of time until the tail was lowered below horizontal with the body.</i>
Piloerection	<i>Fur visibly raised within 0.5 m of the cue (within close proximity). Recorded the duration of time until the fur was no longer visibly raised.</i>
Recruitment Call	<i>The recruitment call type (low or high urgency) given in response to the cue presentation.</i>

Acoustic analysis

Acoustic recordings were analysed using RavenLite to determine the type of recruitment call given (high or low urgency) in response to the presentation (Bioacoustics Research Program 2016). Recruitment call urgency was determined based on the acoustic structure (outlined and defined in: Manser 2001; Manser *et al.* 2001). The duration of the calling bout was also recorded, from the first call given to the last. Due to the nature of the audio recording method it was not possible to determine which individual was calling or how many individuals were calling.

Statistical analysis

Statistical analysis was conducted using R version 1.1.463 (R Core Team 2015), with the packages *lme4* for GLMMs and *TidyVerse* for plotting. Generalised mixed model analyses were conducted on the group level response with group as a random term for analysis a and on individual responses with individual and group ID as random terms for analyses b-g. Analysis was conducted on the behavioural responses of all non-pup (juvenile, sub-adults, adult; hereby referred to as adults) individuals present for the experimental predator cue presentations.

All models (a-g) included the explanatory terms: treatment (NP, PP1, PP2, PP3), cue type (fur, urine), number of pups and number of adult (> 3 months) group members. As individuals' responses may have also been influenced by their group mates' behaviour, I also fitted the proportion of the group interacting with the cue (b-g) and the highest urgency level of call type heard in the group before each focal individual was recruited as additional explanatory terms (a-g). As the original target individual to

whom I originally presented the cue could, by definition, not have heard any prior calls made in response to the cue, call type was categorised as original target individual, no call, low urgency or high urgency. For the analysis (b), whether or not an individual interacted with the cue, if an individual present in the group did not interact with the predator cue presentation, explanatory terms were overall proportion of the group interacting and the highest level call type heard. Individual age (juvenile, sub-adult, adult), sex, and dominance rank (dominant/subordinate) were initially included in the models but removed to reduce model complexity, as they never ranked in the top five models with the lowest AIC values during model selection. *A priori* combinations of fixed effects were used in model building based on biological-relevance.

As the number of pups in the NP treatment was, by definition, zero, the effects of treatment and number of pups could be correlated. To address this, we also ran the analysis with the results of the NP treatment excluded. The results of these models were qualitatively very similar to those conducted on the full dataset (see supplementary material, Appendix 1 Table 1)

Group-level response

First, I analysed the influence of treatment, cue type, number of adults and number of pups on the group level response of (model a). I used a GLMM with binomial error structure, fitting the proportion of the number of individuals responding and number of individuals not responding in the group, to take into account variation in group size. For this analysis I grouped the call types, low urgency and no recruitment, to allow model convergence as there were only two instances of recruitment following no recruitment calls. These two categories were grouped as they are both representative of a lower perceived risk.

Individual response

I then used GLMM's to examine the factors influencing individual behaviour. I conducted a GLMM with binomial error structure and logit link function to examine how the explanatory terms outlined above, influence whether or not an individual interacted with the cue using a binary (0/1) response term (model b). I excluded the response of the original target individual presented to from this analysis as this interaction signified

the beginning of the trial. Among those individuals that did interact, I examined the factors influencing the duration of interactions using a GLMM with a gamma error structure, for over-dispersed continuous data (Zuur *et al.* 2009; Richards *et al.* 2011), and log link function (model c). I also examined whether or not each of these interacting individuals raised their tail as a binary response term (0/1) using a GLMM with binomial error structure and logit link function (model d). For model d I grouped low urgency and no recruitment calls to allow model convergence, as there were only two instances of individuals raising their tails following no recruitment calls. Among those individuals that did raise their tails, I examined the factors influencing the duration of individual's tail raising using a GLMM with a gamma error structure and inverse link function (model e). I also examined whether or not the interacting individuals piloerected as a binary response term (0/1), using a GLMM with a binomial error structure and logit link function (model f). This analysis did not include call type, as no individual showed piloerection if no recruitment calls or low urgency calls had been heard in the group. Among those individuals that did piloerect, I examined the duration of piloerection using a GLMM with a gamma error structure and log link function (model g).

I applied an information theoretic (IT) approach for model selection, using Akaike's information criterion (AIC) to rank the models following the approach used by Richards *et al.* (Richards *et al.* 2011). Models within $AIC \leq 6$ of the model with the lowest AIC value formed the 'top set'. I applied the 'nesting rule' to the top set, removing more complex versions of nested models from the top set so as to not retain overly complex models.

Results

Responses of pups

At least one pup interacted with the cue presentation in 14/18 trials. Of 51 observations, representative of every pup in every trial contributing an observation, there were 19 instances of pups interacting with the predator cues. On average 0.37 ± 0.05 pups were recruited to the predator cues. Pups' interactions lasted an average of 46.10 ± 9.02 seconds. Among the pups that did interact 15/19 did raise their tails for on average 24.40 ± 8.51 seconds, and 5/19 piloerected for on average 14.36 ± 4.78 seconds.

Responses to control vs experimental stimuli

In response to experimental SPCs individuals typically displayed a combination of responses of: approaching the stimuli, investigation of the cue (visually assessing, touching with paws and sniffing), recruitment calls, tail raising, piloerection, and in some cases head bobbing and rocking body movements. In total there were 48 experimental cue presentations and in 25 cases a target individual did not respond after being presented the cue three times. For 6 out of the 24 experimental trials analysed, cues need to be presented more than once to elicit a response. There was only one instance in which all group members did not respond following three SPC presentations. Individuals never reacted to control presentations with more than a brief investigation and only those directly being presented with the control did interact with it. No recruitment calls were given to control cues and no individuals were recruited. Of the 24 control presentations 19 individuals interacted with the control cue, as defined in Table 2, and five did not interact with the cue at all after being presented to three times. Of those that did interact with the control cue, interactions lasted on average 3.77 ± 0.63 seconds, ranging between 0.75-11.25 seconds. Of the 19 individuals that did interact with the control cue only 4 raised their tails for an average of 3.88 ± 1.16 seconds and none piloerected. Mean interaction duration with predator cues (29.66 ± 2.64 seconds) lasted approximately eight times longer than control cue interactions (paired t-test, $t_{23} = 6.587$, $p < 0.001$). Control presentations were not included in the models due to this consistent lack of response.

Group-level responses to SPCs

(a) Proportion of the group recruited

On average 0.34 ± 0.02 of adults in the group were recruited to the predator cue presentations. GLMM analyses produced six models in the top set, of which one (model a.5; Appendix 1 Table 3) was retained with the lowest AIC value. This model contained only the number of pups present in the group as a negative predictor of the proportion of the adults in the group recruited (GLMM: estimate (SE) = $-0.201(0.107)$, $z = -1.884$, $p = 0.06$; Fig. 2.1; Appendix 1 Table 2). Call type appears in the second highest-ranked model but did not have a robust effect (GLMM: estimate (SE) = $0.567(0.573)$, $z = 0.99$, $p = 0.32$)

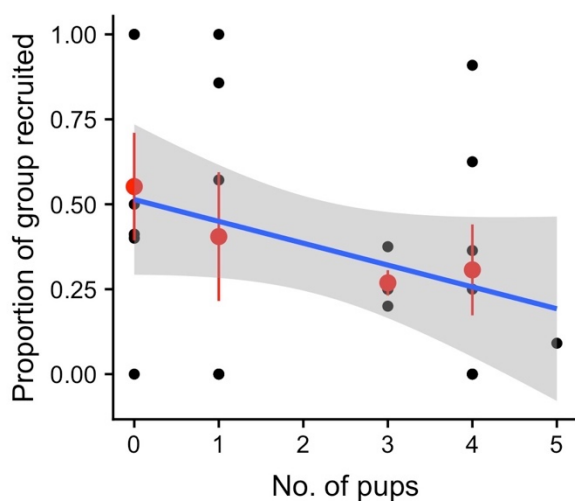


Figure 2.1. The overall proportion of the group recruited dependent on the number of pups present in the group ($n = 24$). Red points indicate the mean proportion recruited with error bars signifying standard error. Blue logistic regression line with the shaded area illustrating the 95% confidence interval.

Individual responses to SPCs

(b) Interacted (y/n)

Of the 202 observations, representative of every individual in every trial contributing an observation, 92 individuals interacted with the predator cue. Out of these 92 cases, 22 were the original target individuals to whom the cue was presented and the remaining 70 were subsequent recruits. GLMM analyses produced three models in the top set, of which one (model b.10; Appendix 1 Table 4) was retained following application of the nesting rule. This model contained only the proportion of the group already interacting with the cue as a positive predictor of whether each new recruit interacted with the cue itself (GLMM: estimate (SE) = $2.992(0.817)$, $z = 3.66$, $p < 0.001$; Fig. 2.2; Appendix 1 Table 2). Call type and treatment (models 9 and 11; Appendix 1

Table 3) appeared in the second and third highest-ranked models respectively, but neither factor appeared to have a robust effect (GLMM; Call type: $X^2 = 1.740$, d.f. = 2, $P = 0.42$; Treatment: $X^2 = 2.686$, d.f. = 3, $P = 0.44$).

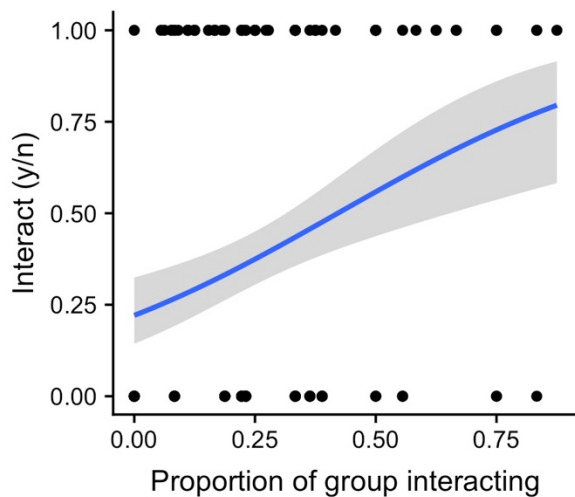


Figure 2.2. The likelihood of an individual interacting with the cue yes ($n = 92$) or no ($n = 110$) dependent on the proportion of individuals in the group already interacting with the cue presentation prior to an individual beginning their interaction. Blue logistic regression line with the shaded area illustrating the 95% confidence interval.

(c) *Interaction duration*

Individuals interacted with the predator cues for on average 29.66 ± 2.64 seconds. GLMM analyses produced three models in the top set, of which one (model 5; Appendix 1 Table 5) was retained following the application of the nesting rule. This model contained only the predator cue type presented, with individuals interacting longer with fur cues, 36.92 ± 3.81 seconds, than urine cues, 23.00 ± 3.40 seconds (GLMM: estimate (SE) = -0.511 (0.169), $z = -3.025$, $p = 0.002$; Fig.2.3a; Appendix 1 Table 2). Treatment appeared both the second and third highest-ranking models having a robust effect when included with number of pups present, with both factors seeming to have an important effect (model 3; treatment: $x^2 = 11.708$, d.f. = 3, $P = 0.008$; number of pups: $x^2 = 5.212$, d.f. = 1, $P = 0.02$; Fig.2.3b Appendix 1 Table 5). There was a positive effect of the number of pups on interaction duration (GLMM; estimate (SE) = 0.243 (0.107), $z = 2.283$, $p = 0.02$; Appendix 1 Table 6). However when treatment was included with cue type the effect of treatment was not robust ($x^2 = 5.357$, d.f. = 3, $P = 0.15$; Fig.3b). Interaction durations were greatest in NP (32.25 ± 5.44 seconds) and PP3 (34.90 ± 4.87 seconds) when cues were novel to the

group and lower in PP1 (25.18±4.50 seconds) and PP2 (23.32±6.54 seconds) when cues were not novel. NP differed most from PP2 (effect size = 0.35, $t = -2.19$, $p = 0.03$; Appendix 1 Table 6), and less from PP1 (effect size = 0.28, $t = -1.09$, $p = 0.27$; Appendix Table 6) and PP3 (effect size = -0.10, $t = -0.63$, $p = 0.53$; Appendix 1 Table 6).

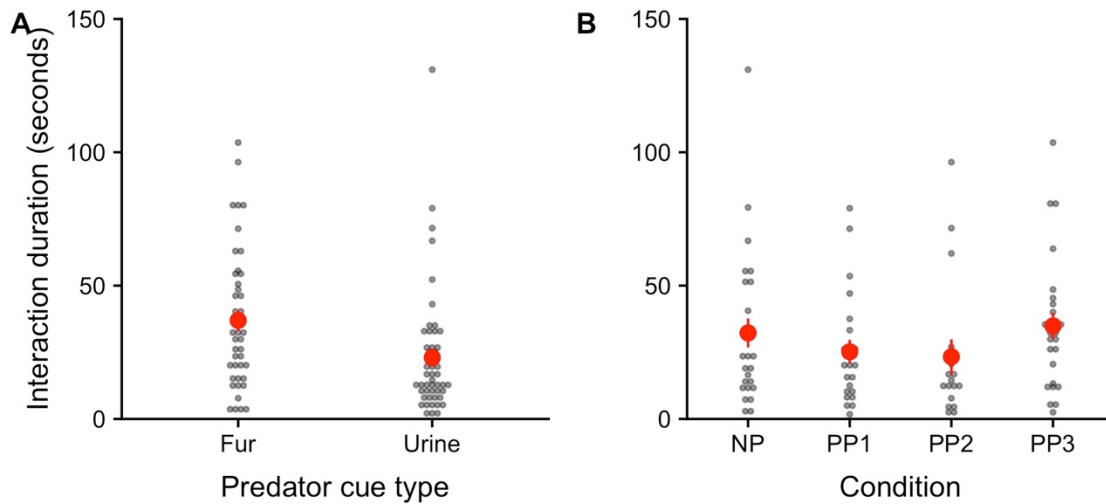


Figure 2.3. The interaction duration in seconds of individuals that did interact with the presentation cues for (a) the two cue types, fur ($n = 44$) and urine ($n = 48$), and (b) for each condition (no pups ($n = 27$), pups present 1 ($n = 22$), pups present 2 ($n = 17$), pups present 3 ($n = 26$)). Red dots indicate the mean interaction duration for each cue type with error bars signifying the standard error.

(d) Tail raised (y/n)

Among those individuals that did interact with the predator cue, 70/92 raised their tails. GLMM analyses produced five models in the top set, of which two (model 4 and model 7: Appendix 1 Table 6) were retained following the application of the nesting rule. Model 4 contained only the number of pups present in the group as a negative predictor of whether an individual would raise their tail (GLMM: estimate (SE) = -0.691 (0.243), $z = -2.84$ $p = 0.004$; Fig.2.4; Appendix 1 Table 2). Model 7 contained only the recruitment call type, with increased probability of individuals raising their tails following a high urgency recruitment call (estimate (SE) = 2.398 (0.818), $z = 2.93$, $P = 0.003$; Appendix 1 Table 1). Number of adults, treatment and proportion recruited (models 13, 8 and 9; Appendix 1 Table 7) also appeared in the top set but did not have a robust effect (GLMM; Number of adults: $\chi^2 = 3.142$, d.f. = 1, $P = 0.076$; Treatment: $\chi^2 = 4.891$, d.f. = 3, $P = 0.180$; Proportion recruited: $\chi^2 = 0.876$, d.f. = 1, $P = 0.35$).

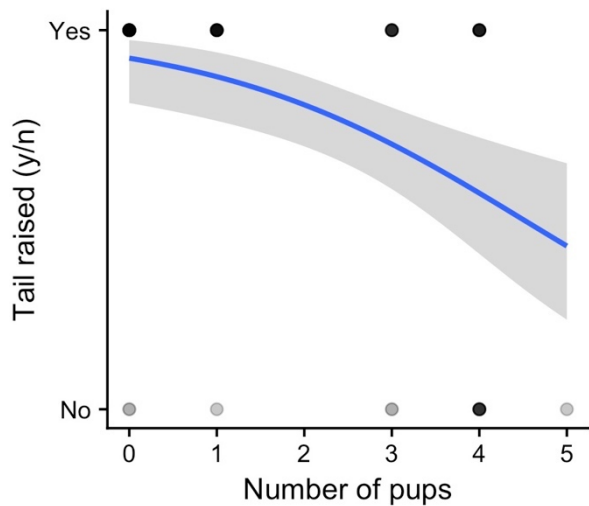


Figure 2.4. The likelihood of an individual interacting with the presentation cue raising their tail yes ($n = 70$) or no ($n = 22$) dependent on the total number of pups present in the. The points shading indicates the frequency of overlapping datapoints. Blue logistic regression line with the shaded area illustrating the 95% confidence interval.

(e) Tail raised duration

The duration that individuals raised their tails for ranged 0.50-57.01 seconds with a mean of 13.89 ± 1.52 seconds. GLMM analyses produced three models in the top set, of which one (model 4; Appendix 1 Table 8) was retained following the application of the nesting rule. This model contained only the number of pups present in the group as a negative predictor of tail raised duration (GLMM: estimate (SE) = $0.016(0.004)$, $z = 3.799$, $p < 0.001$; Fig.2.5; Appendix 1 Table 2). Tail raised duration was greatest when there were no pups present, 20.52 ± 3.28 seconds, and lowest when there were four pups present, 5.09 ± 1.17 seconds. Number of adults and treatment (models 13 and 3; Appendix 1 Table 8) also appeared in the top set but did not have a robust effect (GLMM; Number of adults: $x^2 = 0.091$, d.f. = 1, $P = 0.763$; Treatment: $x^2 = 2.322$, d.f. = 3, $P = 0.508$).

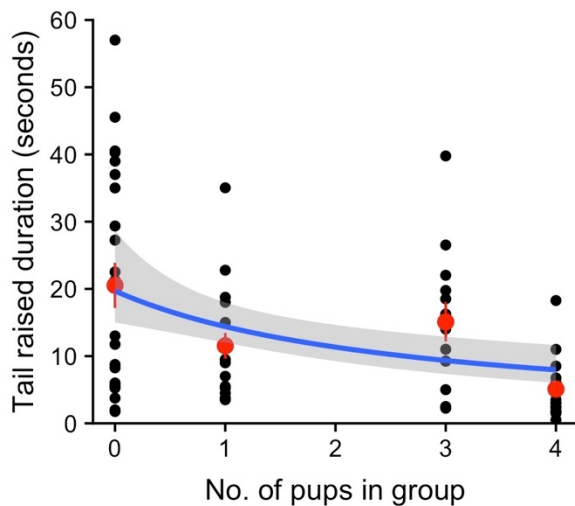


Figure 2.5. The duration that an individual raised their tail for of those that did raise their tail during an interaction with the predator cue ($n = 70$) dependent on the total number of pups present in the group. Red points indicate mean tail raised duration with error bars signifying standard error. Blue linear regression line with the shaded area illustrating the 95% confidence interval.

(f) *Piloerection (y/n)*

Of the 92 individuals interacting with the cues 38 individuals piloerected, 7/38 when interacting with a fur cue and 31/38 when interacting with a urine cue. GLMM analyses produced four models in the top set, of which two (model 5 and 10; Appendix 1 Table 9) were retained following application of the nesting rule. Model 5 contained only the predator cue type, with individuals more likely to piloerect when interacting with a urine cue than a fur cue (GLMM: estimate (SE) = 2.333(0.701), $z = 3.330$, $p < 0.001$; Fig.2.6; Appendix 1 Table 2). Model 10 contained only the proportion of adults recruited as a negative predictor of whether an individual piloerected (estimate (SE) = 5.359, (1.766), $z = -3.03$, $P = 0.002$). Treatment did appear in the top set (model 11; Appendix 1 Table 8) but did not have a robust effect ($\chi^2 = 3.719$, d.f. = 3, $P = 0.29$). Individuals never piloerected following a low urgency or no recruitment call.

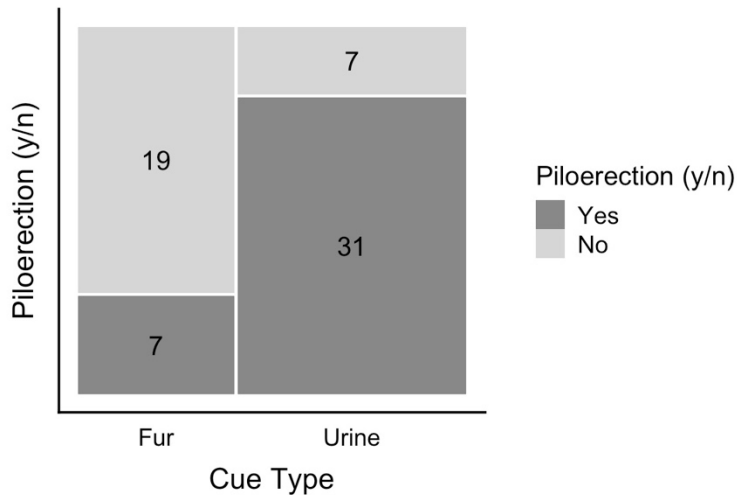


Figure 2.6. The number of individuals that piloerected yes ($n = 38$) or no ($n = 54$) of those individuals interacting with the cue presentation that did piloerect for the two cue types, fur or urine. Dark grey shading indicates those individuals that did piloerect and light grey those that did not. The count for each is displayed within bar.

(g) *Piloerection duration*

Piloerection duration ranged from 2.25-62.01 seconds with a mean duration of 19.42 ± 2.26 seconds. GLMM analyses produced four models in the top set, of which two (model 13 & model 2; Appendix 1 Table 10) were retained. Model 13 contained the number of adults and number of pups present in the group. There was a positive relationship between piloerection duration and the number of adults (estimate (SE) = $0.123 (0.038)$, $z = 3.212$, $p = 0.001$; Fig.2.7a; Appendix 1 Table 2). There was a negative relationship between the piloerection duration and the number of pups (estimate (SE) = $-0.189(0.060)$, $z = -3.161$, $p = 0.002$; Fig.2.7b; Appendix 1 Table 2). Model 2 containing only treatment also appeared in the top set and had a negative effect on piloerection duration, individuals piloerected for shorter durations when pups were present (PP1, PP2, PP3) compared to when no pups were present (NP) (Appendix 1 Table 2). Piloerection durations were greatest in NP (29.94 ± 54.97 seconds) and lower for all pup present treatments, PP1 (13.45 ± 2.67 ; effect size = -1.17 , $t = -4.21$, $p < 0.001$; Appendix 1 Table 11), PP2 (17.73 ± 4.70 ; effect size = -0.86 , $t = -3.66$, $p < 0.001$; Appendix 1 Table 11), and PP3 (13.94 ± 2.91 ; effect size = -1.13 , $t = -4.18$, $p < 0.001$; Appendix 1 Table 11).

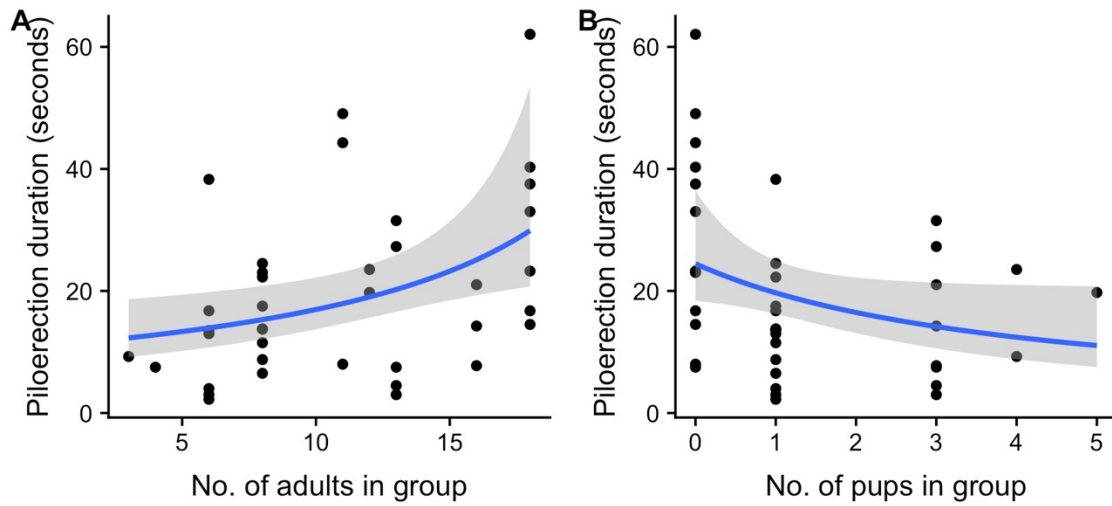


Figure 2.7. The piloerection duration for individuals interacting with the cue presentations that did piloerect ($n = 38$) dependent on (a) the total number of adults present in the group and, (b) the total number of pups present in the group. Blue linear regression line with the shaded area illustrating the 95% confidence interval.

Discussion

The inspection response given to secondary predator cues in meerkats closely resembling the mobbing of alive predators seems rather perplexing, given that unlike most instances of mobbing seen in the animal kingdom, it cannot help to drive predators away. When testing whether adults may instead use exaggerated mobbing-like responses to SPCs to teach naïve pups, my results provided no evidence that this is the case. Adults did not increase the intensity of mobbing in the presence of pups or adjust their mobbing according to pups' experience with the cues. Contrary to my predictions, I found evidence that adults actually reduced their mobbing intensity when pups were present, particularly when more pups were present. These results strongly suggest that the function of mobbing SPCs is not teaching. Instead, the evidence indicates that this behaviour may play a role transferring more detailed information to other group members to aid risk appropriate defensive responses.

I predicted that adults would exaggerate their mobbing-like response when pups were present and foraging with the group, rather than when pups were left at the burrow with a babysitter, and that responses would be particularly exaggerated when cues were novel to pups. None of my analyses supported these predictions, as experimental treatment (NP, PP1, PP2, PP3 where PP3 was always a novel cue) did not appear to influence the proportion of the group recruited, whether or not recruits interacted with the cue, whether interacting individuals raised their tails or piloerected, or the duration of tail raising. Experimental treatment did appear to somewhat affect interaction and piloerection duration, with interaction duration greatest when cues were novel to the group, suggestive of possible habituation through order effects. This habituation seems to have broken when a new cue was presented, returning response duration to the same baseline regardless of whether pups were present. It therefore seems likely that interaction and tail raising duration were related to cue familiarity and presentation order rather than the presence or absence of pups. Piloerection duration, an indicator of intensity, was reduced in the presence of pups unrelated to cue novelty suggesting an overall effect of pups in reducing response intensity. In the analyses of proportion recruited, whether or not an interacting individual raised their tail, and the duration of tail raising and piloerection, larger numbers of pups appeared to have an inhibitory effect on response intensity. The effect of the number of pups was reduced

when the NP treatment was excluded from the analysis for the proportion of the group recruited, whether an individual raised their tail and piloerection duration, but maintained for tail raising duration. This may suggest that it is the presence of pups alone rather than the increasing number that drives this effect in the full dataset. The reduction in intensity maybe reflective of the additional costs associated with provisioning pups, limiting investment in other activities. Alternatively, the high intensity of a mobbing-like response is by definition conspicuous; therefore reducing intensity when vulnerable pups are present may reduce conspicuousness and risk to pups in an area of higher perceived predation risk. Thus, although meerkats are known to teach their pups how to hunt effectively (Thornton & McAuliffe 2006), they do not seem to be use SPCs in teaching to help pups learn about potential predators.

The mobbing-like response to SPCs does not appear to function in teaching naïve pups, leaving the function of this behaviour unresolved. One possible explanation is that mobbing-like response to SPCs is a maladaptive by-product of arousal. Individuals clearly responded to the SPCs as threats, behaving similarly to how they would respond to a predator (Graw & Manser 2007), and showing minimal response to the control cues. This high intensity response to SPCs may represent a misidentification of a SPC as an actual threat. If the mobbing-like response to SPCs was an incorrect response to the stimuli it would be expected that upon determining the cue was not a threat individuals would cease responding in this way. However, this was not the case, individuals tended to continue the mobbing-like behaviours whilst investigating the cues directly sniffing and scratching them, suggesting no error in classification and an awareness that the cue itself is not a threat or predator. Although the mobbing-like response to SPCs is without some of the major costs associated with mobbing (injury, death), there are still substantial energetic, time, opportunity and conspicuousness costs of mobbing, illustrated by the reduction of response intensity potentially due to the additional costs posed by pups. If there were no benefit gained from the mobbing-like response to SPCs it would be expected that selection would act against the persistence of this behaviour.

A more plausible explanation is that the mobbing-like response to SPCs could play a role in information transfer, increasing group awareness of the potential threat and allowing them to gain more detailed, first-hand information on the nature of a threat. A

mobbing-like response may function in increasing the probability of individuals recruiting, providing a conspicuous localisable signal of risk. My results indicate an increased probability of individuals recruiting when a higher proportion of the group are already interacting with the cue, providing a more noticeable event to recruit to. In larger groups where individuals may be more dispersed (Focardi & Pecchioli 2005) signals may need to be more conspicuous to increase the probability of others receiving the signal. This is supported by my result that individuals in larger groups also piloerected for longer, possibly exaggerating response to increase event conspicuousness. A higher number of better informed individuals may be more likely to employ an appropriate defensive response and effectively reduce risk of predation. Juvenile convict cichlids, *Archocentrus nigrofasciatus*, show variation in the level of risk graded responses to conspecific alarm cues (Roh *et al.* 2006). In larger groups, with a greater number of individuals to assess risk, cue concentration indicative of risk posed determines level of response, whereas lone individuals or smaller groups respond to any cue concentration with a more generalised high-risk response.

The raising of group knowledge and alertness through recruitment to SPCs can reduce risk to all members, raising vigilance and increasing speed of potential predator detection (Zöttl *et al.* 2013). Inspection of cues may increase individual knowledge on the type of threat thus facilitating more targeted predator detection. For example, stoats, *Mustela erminea*, respond with differences in scanning behaviour dependent on the source of the scent and effectiveness of the defensive response (Garvey *et al.* 2016). They exhibit greater scanning in response to cat odour, a greater threat above ground, than to ferret, a greater threat below ground. While previous work on meerkats has demonstrated a reduction in detection latency of a nearby predator model following an SPC encounter, predator detection was not necessarily by an individual that had interacted with the cue and benefitting from this additional information. Further work is needed to examine the possible benefits that first-hand investigation of a predator cue provides, and how this information may alter predator detection behaviour. Assessing whether defensive responses differ between investigators and non-investigators and whether responses are targeted dependent on the type of predator, such as vigilance directed to certain habitat types, could shed light on how information from SPCs informs defensive behaviours.

The recruitment to and transfer of information from SPCs could also act in improving group cohesion under increased perceived predation risk. The recruitment of individuals to an SPC may act in bringing the group into greater proximity and enabling coordinated movement away from the area. Exposure of convict cichlids to conspecific alarm cues decreased distance between individuals, improving shoal cohesion (Brown & Foam 2004). When foraging as part of a group cohesive movement is necessary to maintain the advantages of group living (Conradt & Roper 2005). Coordination may be required in initiating and directing group movement away from an area of increased risk. Quorum sensing, in which a minimum number of group members need to take or favour a particular action for the whole group to adopt that action (Conradt & Roper 2005), is used by many species in coordinating group movement decisions (Pratt & Sumpter 2006; Ward *et al.* 2008; Wolf *et al.* 2013; Walker *et al.* 2017). In the mobbing of SPCs a threshold number of individuals may need to be reached to corroborate whether the risk indicated by the SPC is severe enough to warrant a shift in foraging location. In meerkats quorum sensing has been demonstrated through the use of 'moving' calls to induce movement to a new foraging patch. It takes at least two but usually three individuals calls signalling their desire to move onto a new patch, likely due to unsuccessful foraging, for group movement to occur (Bousquet *et al.* 2011). Further work is needed in to assess changes in group cohesiveness and movement, and use of move calls following SPC mobbing events. This could be examined by looking at changes in group members proximity to one another, speed and direction of movement, and changes in move call frequency following SPC encounters.

The lack of evidence for teaching in this context may provide support for the idea that in contrast to human teaching, which occurs across many contexts, non-human teaching is an adaptation to promote context-specific learning (Thornton & Raihani 2008). However further research needs to be conducted on possible candidate behaviours for teaching in non-human animals to assess whether humans are the only species to perform flexible multi-context teaching. Teaching has evolved in other species when acquisition of information or a behaviour by asocial or passive social learning would be slow/dangerous or not occur at all. In the context of mobbing SPCs, pups may have ample opportunities to learn this behaviour by watching adults' responses, as shown in pups' learning of responses to alarm calls (Hollén & Manser 2006; Hollén *et al.* 2008), so there is no benefit for adults modifying their behaviour to

promote learning. The mobbing-like response to SPCs could instead serve to promote group-level responses, increasing vigilance and improving cohesion in the vicinity of a potential threat. Understanding how animals use and interpret information from SPCs provides insight into how information from various sources can shape defensive behaviours.

Chapter Three: Behavioural changes following secondary predator cue recruitment in meerkats

*The accurate assessment of current risk is essential in informing defensive behaviours. Animals use cues left behind by predators, known as secondary predator cues (SPCs), to assess risk and respond appropriately. Many animals use SPCs in this way, however meerkats, *Suricata suricatta*, respond in a seemingly unique way with a mobbing-like response to these cues. The function of this high intensity response remains unclear, as unlike genuine mobbing, it cannot help to drive the predator away. One possible function is that the mobbing-like response facilitates pup learning about possible threats. Alternatively, the response may function in promoting subsequent information gathering by the rest of the group about the nature of the threat. To examine the potential functions I first investigated how meerkats' responses to SPCs differs from mobbing of an actual predator, comparing rate of animal mobbing vs the mobbing-like response to SPCs. Secondly I investigated changes in behaviour (alarm calling, guarding, distance travelled and pup provisioning) in the hour before and after a SPC encounter. I also investigated the effect of the presence of pups on both of these responses. The presence of pups reduced response rate to SPCs, but had no effect on animal mobbing rate, suggesting that responding to SPCs is not a form of teaching. Alarm calling rate was increased and distance travelled decreased following a SPC encounter but were not affected by the presence of pups, suggesting that these are direct responses encountering SPCs. However, guarding rate increased with presence of pups and pup provisioning rate reduced with greater numbers of pups in the group but was not influenced by the recruitment event, indicating that these behaviours are maintained regardless of current perceived risk. Overall, the results suggest that the mobbing-like response to SPCs does not function in teaching pups, but are used in informing group behaviour.*

Introduction

Defensive responses in the face of predation are vital to survival. However, animals typically face trade-offs between defensive responses and other behaviours, such as foraging (Lima & Dill 1990; Verdolin 2006). Assessment of current risk is therefore essential in informing appropriate anti-predator responses reducing time and energy wasted (Lima & Dill 1990). Animals can use a range of cues to inform their defensive behaviours in the face of predation risk (Lima & Dill 1990; Thorson *et al.* 1998). These can be through the direct presence of a predator through visual or acoustic cues, indirect indicators of increased risk such as time of day, habitat type and conspecific remains, or secondary predator cues. Secondary predator cues (SPCs) are cues left in the environment by a predator. These cues are produced by the predator and include predator urine, faeces, fur, regurgitation pellets, scent markings and feathers. The importance of SPCs in informing subsequent defensive behaviours remains unclear.

The use of SPCs can be beneficial in obtaining information about the threat posed without dangerous direct exposure to a predator. Assessment accuracy of predation risk using SPCs is lower than direct predator cues in terms determining the exact nature of the threat, and exact spatial or temporal information. On the other hand, SPCs may provide more precise information on the type of predator and how recently it was in the area than indirect predator cues, such as abiotic conditions associated with increased predation risk. Studies have shown that prey species are able to extract varied information from SPCs, including predator type (Van Buskirk 2001; McGregor *et al.* 2002; Mella *et al.* 2014), predator size (Kusch *et al.* 2004), predator density and proximity (Ferrari *et al.* 2006b), predator diet (Mathis & Smith 1993; Apfelbach *et al.* 2015) and how recently the predator may have been in the area (Barnes *et al.* 2002; Zöttl *et al.* 2013; Kuijper *et al.* 2014; Van Buskirk *et al.* 2014). Using the risk assessment derived from SPCs animals display a whole host of behavioural defensive responses. The most common responses are cue avoidance (Caine & Weldon 1989; Grostal & Dicke 1999; Sike & Rózsa 2006; Roth *et al.* 2008; Amo *et al.* 2011; Severud *et al.* 2011; Apfelbach *et al.* 2015; Weiss *et al.* 2015) and increased vigilance (Monclús *et al.* 2005; Zidar & Løvlie 2012; Zöttl *et al.* 2013; Kuijper *et al.* 2014; Garvey *et al.* 2016; Tanis *et al.* 2018). In some cases, rather than avoiding a SPC, animals will

approach and inspect the cue, gathering more information (Belton *et al.* 2007; Furrer & Manser 2009a; Zöttl *et al.* 2013; Mella *et al.* 2014; Garvey *et al.* 2016). Although animals have been shown to extract detailed information from SPCs and display a range of behavioural responses, the importance of this information in informing behaviour and the fitness benefits conferred remain unclear.

One such behavioural response to SPCs where the function remains uncertain is the mobbing-like response shown in meerkats, *Suricata suricatta*. Several social mongoose species, including meerkats, also recruit other group members upon encountering SPCs, which is thought to act in alerting others to the risk and increase vigilance (Furrer & Manser 2009a; Zöttl *et al.* 2013; Collier *et al.* 2017). When meerkats encounter SPCs they not only recruit other group members but also respond in a similar way to encountering a live predator. This mobbing-like response of tail raising, piloerection and recruitment calls is a seemingly disproportionate response to something that in itself does not pose a threat. The function of this overt reaction is unclear, as it does not provide the primary benefit that mobbing of an actual predator does: driving a threat away (Curio *et al.* 1978b; Graw & Manser 2007). One possible aspect this high-intensity response is that it functions in teaching naïve pups how to recognise cues associated with increased risk and how to respond appropriately. In line with Caro & Hauser's definition of teaching, knowledgeable individuals modify their behaviour in the presence of naïve observers to promote learning with no immediate benefits to themselves (Caro & Hauser 1992). The mobbing-like response to SPCs could be considered teaching if adults increased the intensity of their response in the presence of pups. However, experimental evidence in Chapter two suggests this is not the case, with adults actually decreasing their response intensity in the presence of pups. Corroboration of this result using natural SPC encounters will provide further evidence of whether this behaviour constitutes a form of teaching.

A second possible function of the unusual mobbing-like response to SPCs is that it may play an important role in informing and influencing subsequent group behaviour. By recruiting group members to investigate these cues this suggests there may be a significance of a group-level response to the increased risk, rather than just an individual one. One of the primary benefits of group living is reduced risk of predation (Krause & Ruxton 2002; Caro 2005). In order to maintain these benefits it may be

necessary for all group members to be informed of current risks. Recruitment to SPCs may allow group members to gather detailed information about the threat through inspection, using this information to inform vigilance behaviours, and aid in increasing group cohesion by bringing group members to a focal point. The mobbing-like response may increase likelihood to recruit by denoting a high-level threat and provide a clear signal to move towards. Previous work has shown that meerkats increase vigilance during and immediately following an experimental SPC encounter (Zöttl *et al.* 2013). This work primarily focused on the immediate effect of the cue encounter and not group-level changes in behaviour. The short-term effects of encountering an SPC may lead to other changes in behaviour, not yet examined, that may improve our understanding of the use and importance of SPCs in informing defensive behaviours.

Meerkats are cooperative breeders living in groups ranging from 3-47, averaging 15 individuals (Clutton-Brock & Manser 2016; Wyman *et al.* 2017). Pups begin foraging with the group at around 20-25 days old (Clutton-Brock & Manser 2016). All group members contribute to offspring care, provisioning pups with food until around three months old (Clutton-Brock & Manser 2016). This period of pup dependence on adults provides ample opportunity for pups learn foraging skills and how to recognise predator related alarm calls (Hollén & Manser 2006; Thornton & McAuliffe 2006; Hollén *et al.* 2008). One such learnt behaviour is how to handle dangerous food items, and is one of only a handful of examples of teaching in animals. Adults teach pups how to deal with dangerous food, such as scorpions, by gradually introducing more intact and alive items as they age and gain experience (Thornton & McAuliffe 2006). Meerkats forage as a cohesive group using a 'vocal-hotspot' through close-calls to remain in proximity to one another and maintain the benefits of group living (Gall & Manser 2017). During foraging there is often a sentinel on guard, undertaking vigilance for the whole group, allowing other group members to reduce vigilance and maximise foraging (Santema & Clutton-Brock 2013; Rauber & Manser 2017). Individuals use and recognise a range of referential alarm calls, including high or low urgency calls for terrestrial or aerial predators and recruitment (Manser 2001; Manser *et al.* 2001).

This study aims to investigate how natural SPC encounters alter subsequent behaviour and whether the presence of pups influences these changes. First examining how and if the mobbing-like response differs from the mobbing of animals,

given the similarity of these behaviours even though they do not share a primary function. I compared the factors influencing the frequency of both responses with the prediction that animal mobbing events would be less affected by environmental conditions due to the vital nature of responding to an imminent threat. Whereas, while responses to SPCs may be common given an increased chance of encounter, responses may more plastic and influenced by current conditions. Responding to SPCs consistently may not be integral and, as reported in Chapter two, individuals may not always recruit others to SPC encounters. To investigate the behavioural changes following a SPC encounter I examined how meerkats' perceived predation risk, vigilance, movement and pup provisioning rate varied between the hour prior and post a SPC recruitment event. It would be expected that if responding to SPCs acted in initiating defensive behaviours, (1) alarm calling rate would increase following an encounter if SPCs are accurate predictors of risk or increase sensitivity to potential threats, due to an increased likelihood of predator encounters. (2) Sentinel behaviour (guarding rate), a cooperative form of vigilance, would also increase due to increased perceived risk. (3) The per hour distance travelled would increase following a mobbing event to move out of an area of higher risk. Finally, (4) pup provisioning rate would decrease following a mobbing event as part of a trade-off with defensive responses. In addition I examined the effect of group composition and size on these four behaviours and the effect of current climatic conditions, to investigate whether behavioural responses were plastic and varied with current social and abiotic conditions.

Methods

Study site & species

This study used behavioural data collected as part of long-term monitoring of the meerkat population at the Kalahari Meerkat Project, Kuruman River Reserve (26°59' S, 21°50' E) in South Africa (Clutton-Brock *et al.* 1998). For detail about habitat and climate see (Russell *et al.* 2002). All individuals were habituated to human observation (< 1m) and identifiable from unique dye mark patterns on their backs (Jordan *et al.* 2007). Life history was known for the majority of individuals from birth, including age, sex and dominance status, with the exception of immigrating individuals. I analysed data from 11/04/1999 to 30/04/2019, using only observations with complete records for each analysis.

Data collection

As part of long-term monitoring, groups were visited at least every three days for a minimum of one hour in either the morning following the group leaving the sleeping burrow and/or the evening prior to the groups return to the sleeping burrow. During sessions *ad libitum* (every time a behaviour occurs; (Altman 1974)) behavioural data was recorded. For definitions of behaviours recorded as part of *ad lib* and other data recorded and analysed as part of this study see Table 3.1.

Table 3.1 – descriptions of data recorded as part of long-term monitoring of the population and analysed as part of this study.

Data recorded	Description
Alarm events	<i>When > 50 % of the group respond to a potential threat. Recording the response given by the majority of the group, responses included: look briefly, watch continuously, move, move to bolthole, move below ground and mob. Also recorded the type of threat responded to.</i>
Guarding bouts	<i>A period of vigilance undertaken by an individual of over 10 seconds from a vantage point, which an individual has gone out of its way to guard from or is making sentinel calls.</i>
Pup provisioning	<i>An individual (non-pup) gives a pup a food item.</i>
GPS location	<i>GPS fixes taken taken from the centre of the group at approximately 15 minute intervals during a session (accuracy: 95% of fixes within 5 m; eTrex H, Garmin International Inc., Olathe, KS, USA). Taken either from the time a group left the sleeping burrow or until the group returned to the sleeping burrow.</i>

Group composition	<i>The number of individuals present in a session, their sex and age class/dominance categories.</i>
Daily maximum temperature (°C)	<i>Daily maximum temperature collected at the Kuruman River Reserve weather station.</i>
Daily rainfall (ml)	<i>Daily total rainfall collected at the Kuruman River Reserve weather station.</i>

Mobbing events were recorded as alarm events (Table 1), and defined as when the group recruits to something with erect fur and tails, making recruitment calls, usually spitting and growling. Meerkats mob a variety of threats, primarily predators such as snakes, wildcats etc., see (Graw & Manser 2007) for detailed list. Meerkats also show a mobbing-like response to scents and objects e.g. fur, predator faeces, predator urine, owl pellet, feather, etc.), these responses were also recorded either as to 'scents' or 'objects'. If the type of threat responded to was not known these were recorded as 'unknown' and excluded from my analyses.

Daily maximum temperature and previous 30 days rainfall were used as indicators of current conditions and food abundance (Thornton 2008; Hodge *et al.* 2009; Wiley & Ridley 2016), and previous nine months rainfall was used as an indicator of the groups' overall condition, in line with previous literature (English *et al.* 2012).

Data analysis

(1) Recruitment event rate

Recruitment event rate to SPCs (scents and objects) and animals (any live predator or non-predator) was calculated per group. Mobbing rate was calculated over a month period dividing the number of mobbing events by the number of hours of adlib data recorded, to control for sampling effort.

(2) Behavioural changes following a SPC recruitment event

To examine behavioural changes following a mobbing event, I compared the hourly number of alarm events, number of guarding bouts, distance travelled by the group and per pup provisioning rate, in the hour before and after a mobbing event. The total number of alarm events to potential threats (as outlined above), excluding mob responses, in an hour was used to indicate changes in actual risk and threat sensitivity. The total number of guarding bouts in an hour period was used to indicate changes in

vigilance and perceived risk. The distance travelled in an hour, calculated from the GPS fixes, was used to determine changes in the rate of movement following a mobbing event. Hourly per pup provisioning rate, the number of pup feed events recorded divided by the number of pups present in the group, was used to assess the effect of a mobbing event on pup feeding behaviour.

Statistical analysis

Statistical analysis was conducted using R version 1.1.463 (R Core Team 2015), with packages *lme4* and *glmmTMB* for mixed models and *TidyVerse* for plotting. An information theoretic (IT) approach was applied for model selection, using Akaike's information criterion (AIC) to rank the models following the approach used by Richards *et al.* (2011). Model building was conducted using combinations of fixed effects defined *a priori*. Models within $AIC \leq 6$ of the model with the lowest AIC value formed the 'top set'. To avoid retaining overly complex models I applied the 'nesting rule', removing more complex versions of nested models from the top set.

(1) Recruitment event rate

Linear mixed models (LMMs) with square-root transformation of response rate, to meet model assumptions of normal data distribution, were used to analyse recruitment event rate of SPCs (models a) and animals (models b). Recruitment rate, calculated as the number of recruitment events divided by the normalised total number of session hours, was square-root transformed prior to analysis to meet model assumptions of normal distribution of residuals. Both models (a and b) included the explanatory terms: group size (the average number of individuals in the group during the month) to determine whether group size affects likelihood to recruit. The average proportion of pups (proportion of the foraging group that were pups) to determine whether the number of pups influences whether individuals recruit. Average sex ratio (mean number of females to males over the month) to examine the group composition may play in recruitment frequency. Whether pups were foraging with the group or not as a binary response was used to test whether pup presence alone was enough to influence recruitment frequency. Average daily maximum temperature (mean daily maximum temperature over the month), total rainfall for the previous 30 days and total rainfall for the previous nine months), were used to test the effect of temperature and

rainfall conditions on recruitment event frequency. Random terms group nested within year were used to control for group effects and differences in durations of groups in the population over the study period.

(2) Behavioural changes following a SPC recruitment event

Generalised linear mixed models (GLMMs) were used to analyse behavioural changes before and after a SPC recruitment event, examining the hourly number of alarm events (c), hourly number of guarding bouts (d), kilometres travelled per hour (e) and hourly per pup provisioning rate (f). Models c-e were fitted with a negative binomial error structure to account for overdispersion of data, and model f was fitted with a zero-inflated negative binomial error structure to account for zero-inflation and overdispersion. The same explanatory terms outlined above were used except sex ratio. Sex ratio was initially included in the analyses but never ranked within the top 5 models with the lowest AIC values during model selection, so was removed to allow more complete records to be analysed. The group size, proportion of pups and daily maximum temperature recorded at the time of the recruitment event were used rather than the monthly average. Model f did not include whether pups were foraging with the group as pup provisioning would only occur if they were present. Models c-f also included whether the response was in the hour before or after the mobbing to test whether there was a behavioural change, and whether the cue type was a scent or an object to examine whether cue type influences changes in behaviour. The interactions of both before/after and the presence of pups with all other fixed effects were used as both these factors may have interacted with the other factors to influence behaviour. The interaction of daily temperature with either 30 day and nine month rainfall was included as temperature and rainfall driven food availability and body condition are generally closely linked. Random terms of group nested within year were also used.

Results

Recruitment event rate

(a) SPC recruitment rate

Data was analysed from 54 groups over 20 years, on 131,289 hours of recorded data over 52,776 sessions. The hourly mobbing rate for each group over a one month period ranged from 0 to 0.28 (mean \pm SE = 0.03 \pm 0.00). LMM analyses produced two models in the top set, both of which were retained following the application of the nesting rule (model a13 and model a12; Appendix 2 Table 2). Model a13 contained the proportion of pups, the average group size for that month and the interaction between the two. The SPC mobbing rate was higher in larger groups (LMM: estimate(SE) = 0.05(0.005), $x^2 = 85.90$, d.f. = 1, $p < 0.001$; Fig.3.1b; Appendix 2 Table 1), but declined as the proportion of pups in the group increased (estimate(SE) = -0.23(0.51), $x^2 = 22.81$, d.f. = 1, $p < 0.001$; Fig.13.a; Appendix 2 Table 1). There was not a robust effect of the interaction between number of pups and group size (estimate(SE) = -0.06(0.04), $x^2 = 2.99$, d.f. = 1, $p = 0.41$; Appendix 2 Table 1). Model a12 contained whether or not pups were foraging with the group, the average group size and the interaction between the two. SPC mobbing rate was reduced when pups were foraging with the group, however the effect appears small in Figure 1c (estimate(SE) = -0.29(0.15), $x^2 = 22.95$, d.f. = 1, $p < 0.001$; Fig.3.1c; Appendix 2 Table 1), but there was no interaction between the presence of pups and group size (pups foraging*group size: estimate(SE) = -0.001(0.008), $x^2 = 0.01$, d.f. = 1, $p = 0.94$; Appendix 2 Table 1).

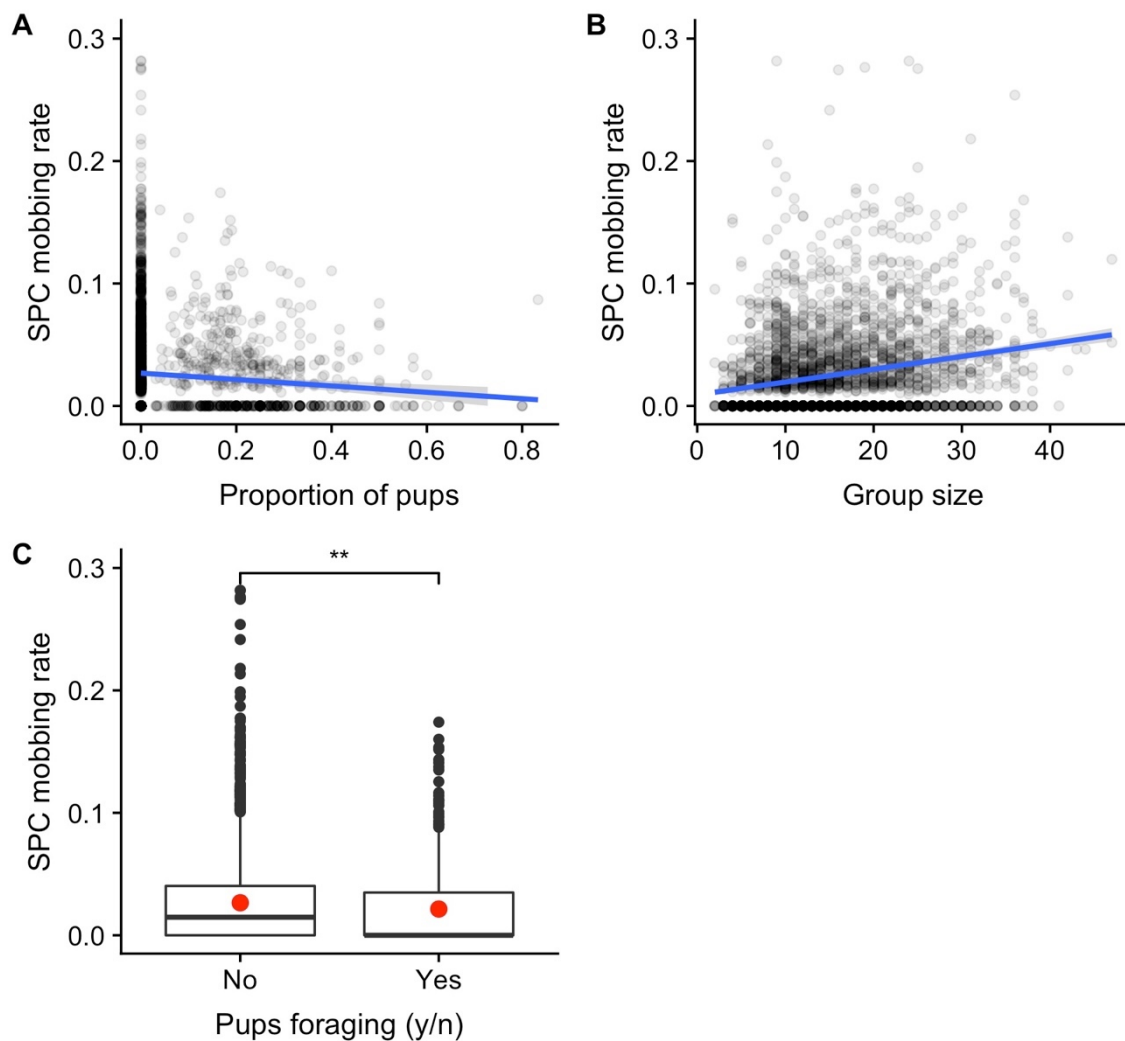


Figure 3.1. – The hourly per group rate of recruitment events in a month to SPCs ($n = 2918$) predicted by (a) proportion of the foraging group made up by pups, (b) total group size, (c) whether pups were foraging with the group (yes ($n = 660$) or no ($n = 2258$)). The shade of points indicates the frequency of data points overlapping. The blue linear regression line with the shaded area illustrates the 95% confidence interval. Red dots indicate the mean rate of recruitment events.

(b) Animal mobbing rate

Meerkat groups mobbed animals between 0 and 0.26 times per hour each month (mean \pm SE = 0.01 \pm 0.00). LMM analyses produced three models in the top set, of which one (model b6; Appendix 2 Table 3) was retained following the application of the nesting rule. Model b6 contained only the average group size as a significant positive predictor of animal mobbing rate (LMM: estimate(SE) = 0.03(0.003), $x^2 = 68.59$, d.f. = 1, $p < 0.001$; Fig.3.2; Appendix 2 Table 1). The proportion of pups as a negative predictor and a slight reduction in mobbing frequency when pups were foraging with the group also appeared in the top set but did not have a robust effect (proportion of pups: estimate(SE) = -0.22(0.39), $x^2 = 2.83$, d.f. = 1, $p = 0.09$; pups foraging:

estimate(SE) = -0.04(0.11), $x^2 = 0.61$, d.f. = 1, $p = 0.44$; Appendix 2 Table 1), and did not interact with average group size (group size*proportion of pups: estimate(SE) = -0.001(0.03), $x^2 = 0.03$, d.f. = 1, $p = 0.87$; group size*pups foraging: estimate(SE) = 0.001(0.01), $x^2 = 0.001$, d.f. = 1, $p = 0.94$; Appendix 2 Table 1).

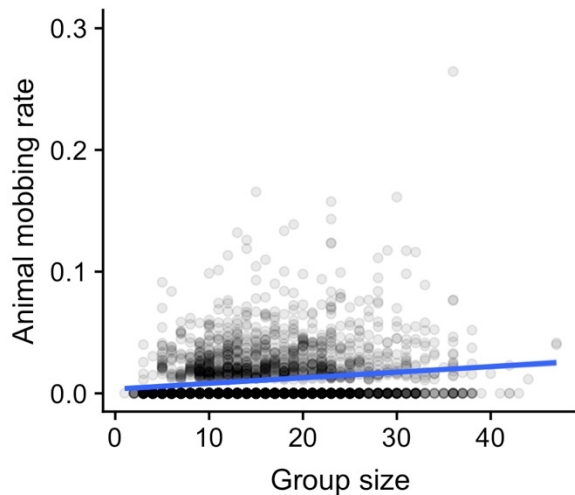


Figure 3.2. – The hourly per group rate of recruitment events in a month to animals predicted by total group size ($n = 2918$). Shade of points indicating frequency of data points overlapping. Blue linear regression line with the shaded area illustrating the 95% confidence interval.

Behavioural changes following a SPC recruitment event

(c) Number of alarm calls

The number of alarm calls ranged from 0-19 over per hour (mean \pm SE = 2.23 \pm 0.03). GLMM analyses produced two models in the top set of which both (model c8 and c12: Appendix 2 Table 5) were retained following the application of the nesting rule. Model c8 contained the hour before and after the mobbing event, the maximum temperature on that day and the interaction between the two. Alarm calling rate increased in the hour after a mobbing event (2.32 \pm 0.04), compared with the hour before (2.14 \pm 0.04) (GLMM: estimate(SE) = 0.03(0.11), $x^2 = 13.34$, d.f. = 1, $p < 0.001$; Fig.3.3a; Appendix 2 Table 3), but declined as the daily maximum temperature increased (estimate(SE) = -0.02(0.003), $x^2 = 73.61$, d.f. = 1, $p < 0.001$; Fig.3.3b; Appendix 2 Table 3). There was no interaction between the time period (before/after) and the daily maximum temperature (before/after*temperature: estimate(SE) = -0.004(0.004), $x^2 = 1.22$, d.f. = 1, $p = 0.27$; Appendix 2 Table 3). Model c12 contained daily maximum temperature,

total rainfall over the last 9 months and the interaction between the two (temperature*rainfall: estimate(SE) = 0.05(0.02), $\chi^2 = 8.09$, d.f. = 1, $p = 0.004$; Fig.3.3c; Appendix 2 Table 3). When rainfall had been high in the previous nine months, the daily maximum temperature had little effect on alarm rate. As nine month rainfall decreased the disparity between alarm calling rate increased, with alarm calling rate greater at low temperatures and reducing at high temperatures.

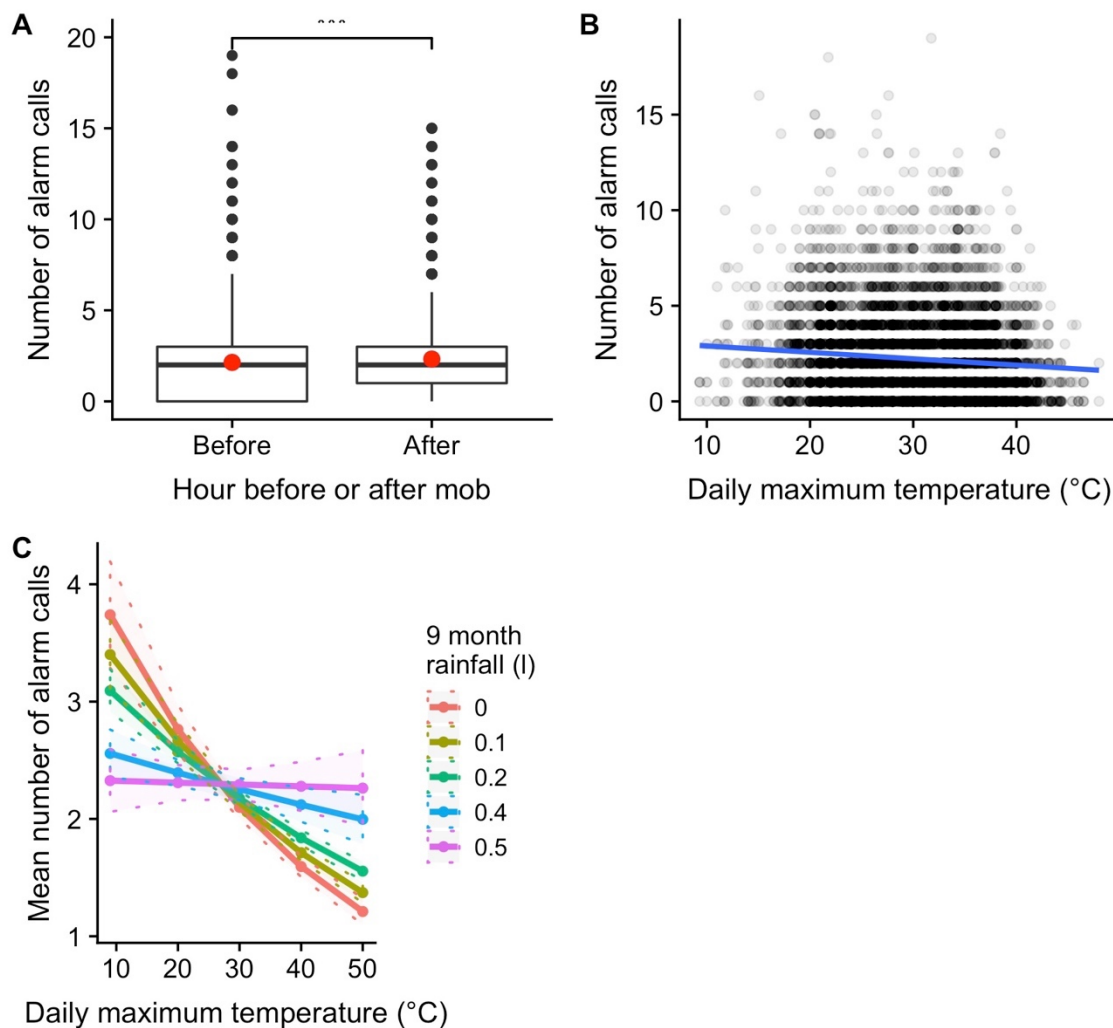


Figure 3.3. – The hourly alarm calling rate ($n = 6946$) predicted by (a) whether it was before ($n = 3473$) or after ($n = 3473$) a SPC recruitment event, (b) daily maximum temperature, (c) interaction between daily maximum temperature and total rainfall over the previous 9 months. Red dots indicating mean rate of recruitment events. Shade of points indicating frequency of data points overlapping. Blue linear regression line with the shaded area illustrating the 95% confidence interval.

(d) Number of guarding bouts

The number of guarding bouts ranged from 0-24 over a one hour period (mean \pm SE = 1.80 ± 0.03). There was no evidence that meerkats increased their rate of guarding in

the hour after encountering a SPC. Instead, GLMM analyses produced one model in the top set following application of the nesting rule (model d18 ; Appendix 2 Table 6). Model d18 contained whether pups were foraging with the group, rainfall for the previous nine months and the interaction between the two (9 month rainfall*pups foraging: estimate(SE) = -0.85(0.33), $x^2 = 6.50$, d.f. = 1, $p = 0.011$; Fig.3.4; Appendix 2 Table 3). Guarding rate increased with greater rainfall over the previous nine months. Overall, guarding rate was higher when pups were foraging with the group. Guarding rate was lower when pups were not foraging with the group, particularly at low rainfall, however there was little difference between when pups were or were not present at high rainfall.

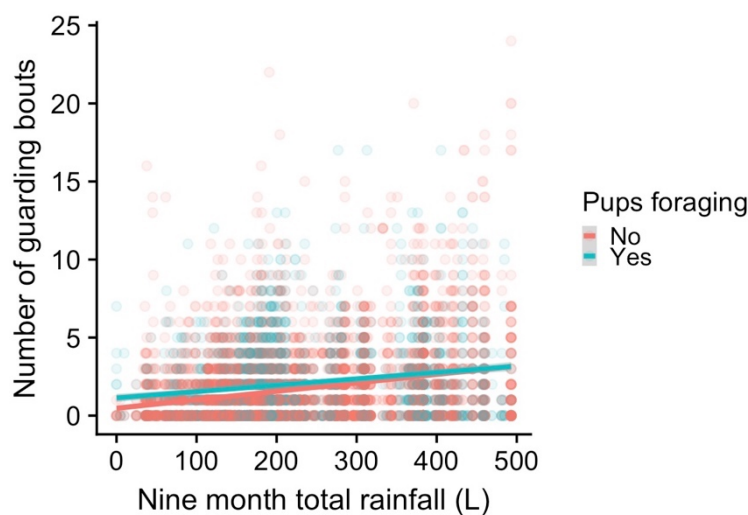


Figure 3.4. – The hourly number of guarding bouts ($n = 6944$) predicted by total rainfall over the last 9 months interacting with whether pups were foraging with the group yes (blue; $n = 1806$) or no (pink; $n = 5138$). Shade of points indicating frequency of data points overlapping. Linear regression lines with the shaded area illustrating the 95% confidence interval.

(e) *Distance travelled*

The distance that meerkat groups travelled ranged from 0-1431m per hour (mean \pm SE = 173.59 \pm 2.10 m). GLMM analyses produced three models in the top set, of which all three (model e8, model e12 and model e13; Appendix 2 Table 7) were retained following the application of the nesting rule. Model e8 contained the hour before or after the mobbing event, daily maximum temperature and the interaction between the two. Meerkats travelled shorter distances in the hour following an SPC encounter than the hour before (GLMM: estimate(SE) = 0.27 (0.17), $x^2 = 18.23$, d.f. = 1, $p < 0.001$; Fig.3.5a; Appendix 2 Table 3), and travelled further as daily maximum temperature

increased (estimate(SE) = 0.02(0.003), $x^2 = 68.11$, d.f. = 1, $p < 0.001$; Fig.3.5b; Appendix 2 Table 3). The interaction between hour before or after and daily maximum temperature was not robust (before/after*temperature: estimate(SE) = -0.01(0.004), $x^2 = 2.15$, d.f. = 1, $p = 0.15$; Appendix 2 Table 3). Model e12 contained daily maximum temperature, total rainfall in the previous nine months and the interaction between the two. Distance travelled reduced as nine month total rainfall increased (estimate(SE) = 0.34(0.69), $x^2 = 13.10$, d.f. = 1, $p < 0.001$; Fig.3.5c; Appendix 2 Table 3). The interaction between nine month rainfall and maximum daily temperature did not have a robust effect (9 month rainfall*temperature: estimate(SE) = -0.03(0.02), $x^2 = 2.47$, d.f. = 1, $p = 0.12$; Appendix 2 Table 3). Model e13 contained daily maximum temperature, total rainfall for the previous 30 days and the interaction between the two. There was an interaction between 30 days rainfall and daily maximum temperature (30 day rainfall*temperature: estimate(SE) = -0.17(0.08), $x^2 = 4.48$, d.f. = 1, $p = 0.03$; Fig. 5d; Appendix 2 Table 3). At low 30 day rainfall distance travelled increased with temperature, at intermediate rainfall there was a slight increase in distance travelled at higher temperatures. Whereas, at very high rainfall distance travelled decreased with increasing temperature.

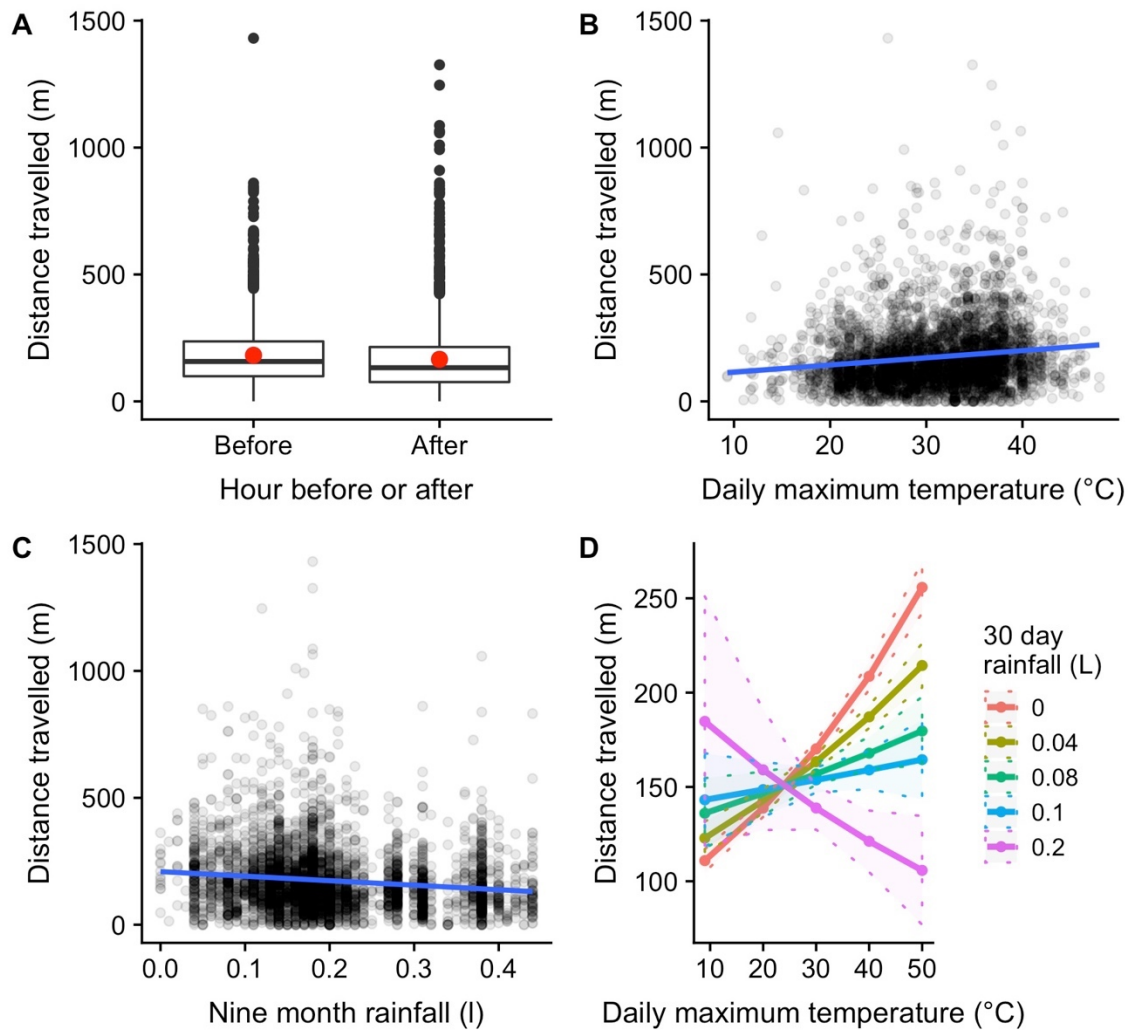


Figure 3.5. – The hourly distance travelled by a group ($n = 4024$) predicted by (a) whether it was the hour before ($n = 2012$) or after ($n = 2012$) a SPC recruitment event, (b) daily maximum temperature, (c) the interaction of daily maximum temperature and total rainfall over the previous 30 days, (d) total rainfall over the previous 9 months. Shade of points indicating frequency of data points overlapping. Linear regression lines with the shaded area illustrating the 95% confidence interval. Red dots indicating mean rate of recruitment events.

(f) *Provisioning rate*

Per pup hourly provisioning rate ranged from 0 to 11.5 (mean \pm SE = 1.20 ± 0.05). GLMM analyses produced three models in the top set, of which one was retained following application of the nesting rule (model f15; Appendix 2 Table 8). Model f15 contained only the proportion of the pups present with per pup provisioning rate decreasing as the proportion of pups increased (GLMM: estimate(SE) = $-2.86(0.63)$, $x^2 = 22.52$, d.f. = 1, $p < 0.001$; Fig.3.6; Appendix Table 3). Total group size and the hour before or after the mob also appeared in the top set but neither had a robust effect (group size: estimate(SE) = $0.01(0.02)$, $x^2 = 1.25$, d.f. = 1, $p = 0.26$; before/after: estimate(SE) = $0.07(0.17)$, $x^2 = 0.23$, d.f. = 1, $p = 0.63$; Appendix 2 Table 3), and

neither interacted with the proportion of pups (group size*proportion of pups: estimate(SE) = -0.15(0.08), $x^2 = 3.61$, d.f. = 1, $p = 0.06$; before/after*proportion of pups: estimate(SE) = -0.15(0.76), $x^2 = 0.04$, d.f. = 1, $p = 0.84$; Appendix 2 Table 3).

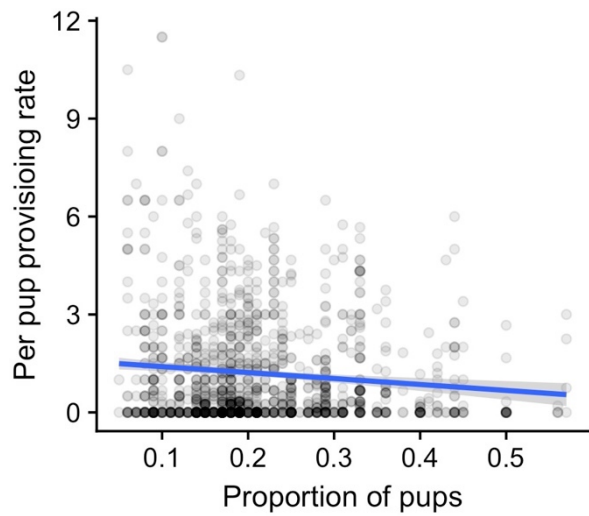


Figure 3.6. – The hourly per pup provisioning rate ($n = 1248$) predicted by the proportion of the foraging group made up by pups. Shade of points indicating frequency of data points overlapping. Blue linear regression line with the shaded area illustrating the 95% confidence interval.

Discussion

SPCs can provide useful information about likely threat levels, but the function of meerkats' highly exaggerated mobbing-like response is unclear. The response closely resembles mobbing yet it does not yield the primary benefit of driving a threat away. I examined two potential functions. One is that mobbing-like responses towards SPCs serve as a form of teaching to help naïve pups to learn about the characteristics of potential predators. The other is that the mobbing-like response facilitates recruitment of group members, raising group knowledge of the threat posed and informing subsequent defensive behaviours. In line with previous work (Chapter two) I found no support for the teaching hypotheses. Instead, a greater number pups reduced frequency of SPC recruitment events and increased guarding rate. Additionally following a SPC encounter alarm calling rate increased and distance travelled decreased, suggesting that SPC interactions do influence group-level defensive behaviours.

The results do not provide support for the mobbing-like response to SPCs acting as a form of teaching. In opposition to what would be predicted if this behaviour did function in teaching, when higher numbers of pups were present frequency of SPC recruitment events reduced, with the presence of pups alone sufficient in reducing event frequency. This is line with the previous findings that the intensity of response to SPCs decreased when pups were foraging with the group (decreased recruitment, tail raising and piloerection duration) (Chapter two). The mobbing-like response to SPCs may be a plastic behaviour influenced by current constraints and conditions. Moreover the lower frequency of SPC recruitment events may be due to only a small number of individuals recruiting ($< 50\%$ of the group), in which case the event would not have been recorded. This is corroborated by the results of Chapter two where over 50% of adults recruited when no pups were present and less than 50% when pups were present. In the previous chapter I suggested a possible reason for the reduction in response intensity was a trade-off between responding to SPCs and provisioning pups. The results of this study support that pup provisioning rate was maintained and not changed by a SPC encounter, with no effect of a SPC recruitment event on per pup provisioning rate. Pup provisioning rate was only constrained by the number of pups in the group, with per pup rate reducing as number of pups increased. This

suggests that investment in the mobbing-like response may be reduced to maintain pup provisioning rate. The inhibitory effect of pup presence on frequency of the mobbing-like response towards SPCs supports that this behaviour does not function in teaching. Thus although meerkats do teach hunting skills, it is still the case that all known examples of teaching in non-human animals occur in a single context, in contrast to humans teaching (Thornton & Raihani 2008).

Instead, some of the results are consistent with the mobbing-like response towards SPCs acting in gathering information and informing subsequent group behaviour. The rate of responding to SPCs and mobbing animals are both positively associated with group size. Large group sizes tend to confer benefits against predation through the safety in numbers effect and increased predator detection (Krause & Ruxton 2002; Caro 2005). For example, larger groups of chestnut-crowned babblers, *Pomatostomus ruficeps*, are more likely to encounter predators but less likely to be attacked (Sorato *et al.* 2012). In defending against predators larger groups have been shown to have greater success and individuals mob with greater intensity (Krams *et al.* 2009). The increase in rate of animal mobbing and mobbing-like response with increasing group size in this study may be due to a greater encounter rate of predators and their cues in larger groups. Alternatively, or additionally, larger groups may be more likely to respond to a predator or their cues with recruitment rather than fleeing, due to the reduced risk to individuals through the dilution and confusion effects (Hamilton 1971; Foster & Treherne 1981; Lehtonen & Jaatinen 2016). Recruiting individuals to the threat may act in informing them of the nature of the threat to better inform the groups collective defensive behaviours. The greater frequency of recruitment events, particularly in regards to SPCs, may be due to difficulties in maintaining group cohesion in larger groups (Focardi & Pecchioli 2005). Recruitment to cues may bring the group to a focal point facilitating informed decision making and cohesive movement away, possibly through quorum sensing. Meerkats have been shown to use quorum sensing in group movement decisions in regards to changing foraging location (Bousquet *et al.* 2011). Increased group cohesion may reduce vulnerability of group members to predation, bringing the group closer together, making it harder for a predator to isolate an individual. White-breasted mesites, *Mesitornis variegatus*, increase group cohesion following an alarm event (Gamero & Kappeler 2015), and convict cichlids, *Amatitlania nigrofasciata*, do so in response to conspecific alarm cues

(Brown & Foam 2004). Whether SPC encounters do result in increased group cohesion in meerkats could be examined by testing whether inter-individual distance changes following a recruitment event.

Also consistent with the role of the mobbing-like response to SPCs in informing subsequent behaviour are the increase in alarm calling rate and decrease in distance travelled in the hour following an SPC encounter. The increase in alarm calling rate following a mobbing-like recruitment event may be suggestive of either an increase in actual risk, i.e. a predator in the vicinity, or increased sensitivity to potential threats. Previous work has shown that predator detection latency reduced following an SPC encounter (Zöttl *et al.* 2013), demonstrating that SPCs may be a reliable indicator of a predator in close-proximity and used in informing defensive behaviours to successfully locate the threat. Increased perceived risk may also increase threat-sensitivity resulting in increased alarm calling. Signal-detection theory predicts that as risk increases the cost of not responding increases, meaning under high perceived risk it may be safer to respond or over-react to a non-threat than risk not reacting (Wiley 2006; Ferrari *et al.* 2009). For example, brushtail possums, *Trichosurus vulpecula*, respond more strongly to SPCs when there is not access to shelter and therefore greater vulnerability to predation (Parsons & Blumstein 2010b). In contrast to our predictions, distance travelled following a SPC encounter reduced, rather than increased to move away from an area of perceived risk. This decrease in distance travelled may be related to the recruitment event itself due to the time taken to respond in a mobbing-like way, with individuals recruiting to a specific area and spending time investigating the cue. The reduced distance travelled may also have been due to an increase in defensive behaviours such as vigilance (Zollner *et al.* 2014), slowing movement in the period following a recruitment event. Although no change in guarding behaviour was found following a SPC encounter.

Not all of the behaviours examined as part of this study changed following an SPC encounter. There was no change in guarding rate following a mobbing-like recruitment event. This may suggest that vigilance does not change as a result of a SPC encounter, contrary to much of the literature (Monclús *et al.* 2005; Zidar & Løvlie 2012; Zöttl *et al.* 2013; Kuijper *et al.* 2014; Garvey *et al.* 2016; Kern *et al.* 2017; Tanis *et al.* 2018). However, although guarding behaviour may not have changed, there may have

been changes in other types of vigilance. The long-term data collected and analysed as part of this study only recorded guarding vigilance; while this particular form of vigilance may not change following an SPC encounter, individual quadrupedal vigilance (scanning on four legs) which was not recorded as part of the long-term monitoring may have increased. In an area of greater risk, as indicated by a SPC, it may be more appropriate for many individuals to be performing scanning vigilance, rather than one sentinel being vigilant for the whole group. This possible increase in individual vigilance may have led to the increase in alarm calls recorded in this study and more rapid predator detection reported in previous studies (Zöttl *et al.* 2013). Further study could examine whether there are changes in frequency and duration of other forms of vigilance (such as quadrupedal scanning) in meerkats following an SPC encounter.

While there was not an effect of a SPC encounter on guarding rate, it was influenced by the presence of pups. Guarding rate was more consistent and generally higher when pups were foraging with the group, consistent with previous work (Santema & Clutton-Brock 2013). This suggests overall perceived risk may be greater when pups are present resulting in higher general vigilance. There was a significant interaction between nine month rainfall (body condition) and the presence of pups on guarding. Overall guarding frequency increased with rainfall, with greater condition dependent variation when pups were not foraging with the group. This suggests that although sentinel bouts are often determined by individual condition and nutritional needs (Clutton-Brock *et al.* 1999; Wright *et al.* 2001), when pups are with the group a higher guarding rate is maintained regardless of individual condition. Vigilance may increase when foraging with pups due to the vulnerable nature of pups, or due to increased conspicuousness of the group as a result of pups' constant begging calls. Higher vigilance can be associated with increased conspicuousness (Blanchard *et al.* 2017) to help protect against increased risk of predation due to the conspicuous nature of begging calls (Haskell 2005; McDonald *et al.* 2009). Pup provisioning rate was not changed following a mobbing-like recruitment event. The consistent rate of provisioning regardless of recruitment to a SPC suggests that although there are other behavioural changes associated with the event, these changes are not part of a trade-off with pup provisioning.

Abiotic conditions seem to have a strong impact on behavioural responses (alarm calling, guarding and distance travelled), generally independent of the recruitment event and the presence of pups. These condition associated effects on behaviour highlight the importance of food availability, climatic environment and individual condition in mediating behaviour. At high maximum daily temperatures alarm calling rate decreased and distance travelled increased. This is suggestive of greater investment in foraging, reducing vigilance as a trade-off resulting in lower alarm calling rate, and having to travel greater distances to locate foraging patches. This is supported by the interaction between temperature and rainfall. Reduction in alarm calling was greatest at high temperatures with lower rainfall in the previous nine months, representative of individuals in poorer body condition. Lower nine-month rainfall also decreased guarding frequency and distance travelled. Those in poor condition may be less able to afford to trade-off foraging opportunities with vigilance, reducing investment in vigilance (Arenz & Leger 2000). Reduction in body condition may also affect individuals' abilities to travel greater distances (Duijns *et al.* 2017). The impact of abiotic conditions implies some plasticity in behavioural responses dependent on nutritional and thermoregulatory needs, and general body condition. Although abiotic conditions did not affect frequency of recruitment events to SPCs, the role of pup presence may suggest a condition dependent effect due to short-term energetic costs associated with pup care (Russell *et al.* 2003).

The function of the mobbing-like response itself remains unclear when recruitment through calling alone would achieve a similar outcome. The additional visual nature of a mobbing-like response, on top of recruitment calls, may increase the efficacy of this response. The high intensity reaction may also increase the likelihood of other group members responding and recruiting to the area in which the cue was encountered. As a result the effectiveness of this response may be increased by ensuring all group members are aware of the threat and take appropriate defensive actions. This could be experimentally tested by investigating whether greater recruitment is observed to a mobbing-like response of SPCs than to a recruitment call alone, and/or if this enhances subsequent behavioural changes following the encounter.

Overall the results indicate SPC encounters do influence subsequent behaviour, increasing alarm calling and decreasing distance travelled. Also the presence of pups

does influence the response to cues, with recruitment event frequency reducing when pups are present. However there was not an interaction between the behavioural changes following a SPC encounter and the presence of pups. The lack of changes in guarding rate and pup provisioning suggest that these behaviours are of vital importance, needing to be maintained independent of the influence of single events. It appears that SPCs are accurate predictors of increased risk, resulting in increased alarm calling, and are used in informing defensive behaviours, indicated by the lower distance travelled following an encounter. The effects of pup presence and abiotic conditions implies there may be a certain degree of plasticity in responding to SPCs. This plasticity may reflect condition dependent use and necessity for using information gathered from SPCs in informing subsequent behaviour.

Chapter Four: General discussion

The mobbing-like response towards SPCs in meerkats is an unusual one. Unlike typical mobbing of a predator, this almost identical response to SPCs does not function in driving the predator away. In theory this could be a non-adaptive by-product of responses to predator stimuli. However, given the substantial time and energy costs involved in mobbing-like responses towards SPCs, one would expect selection to have acted against an erroneous overreaction. In this thesis, I examined one potential adaptive function for the maintenance of this behaviour: perhaps it functions to teach pups how to recognise and respond to cues associated with predators. Contrary to my predictions, evidence from both experiments and long-term behavioural monitoring converges on the conclusion that this mobbing-like response is not a form of teaching.

In Chapter two I used targeted experimental presentations to test whether adults increase response intensity towards SPCs in the presence of pups - a key criterion if the behaviour is to be considered as a form of teaching (Caro & Hauser 1992). Contrary to predictions I found that the presence of pups did not increase the intensity of the mobbing-like response, but instead greater numbers of pups appeared to have an inhibitory effect. Specifically, experimental treatments comparing whether or not pups were foraging with the group did not appear to influence the proportion of the group recruited, whether or not recruits interacted with the cue, whether interacting individuals raised their tails or piloerected, or the duration of tail raising. Additionally, response intensity decreased as the number of pups present increased, with reductions in the proportion of the group recruited, whether or not interacting individuals raised their tail, and the duration of tail raising and piloerection.

In Chapter three I then used long-term behavioural data (from 54 groups over 20 years, on 131,289 hours of recorded data over 52,776 sessions) to investigate how mobbing of live predators differs from the mobbing-like response towards SPCs, testing the factors affecting natural response rate. I also examined whether SPC encounters resulted in behavioural changes in alarm calling rate, guarding frequency, distance travelled and pup provisioning rate. Again, the presence and number of pups had a limiting effect, reducing SPC response frequency, and also had little effect on behavioural changes in the hour following a SPC encounter. The presence of pups

increased guarding rate generally but did not affect behavioural changes following an SPC encounter. Alarm calling rate was increased and distance travelled decreased following a SPC encounter but was not affected by the presence of pups, suggesting these are direct responses to encountering SPCs. These results from both the experimental and natural SPC encounters showing that presence of pups has either a negative or no effect, support the conclusion that the mobbing-like response does not function in teaching. Instead the results suggest that this behaviour acts in the transfer of information to group members, helping to inform group defensive behaviours. In what follows, I will consider the implications the lack of evidence for teaching has on our understanding of the evolution of non-human teaching. Additionally, I will discuss the alternative potential advantages the mobbing-like response to SPCs provides, given it does not appear to function in teaching .

Implications for the evolution of teaching

So far, all evidence for teaching in non-human animals occurs only in a single context (Thornton & Raihani 2008). This is in stark contrast to human teaching, which occurs across an almost infinite number of situations and contexts (Thornton & Raihani 2008; Kline 2015). Teaching is defined as a knowledgeable individual modifying their behaviour at some cost or with no immediate benefit so as to promote learning in others (Caro & Hauser 1992). Teaching has been documented in invertebrates, birds and mammals, but in every species it appears to be an adaptation for solving one particular problem, or developing a specific skill. For instance, tandem-running ants, *Temnothorax albipennis*, teach group members routes from the nest to food using tandem running (Franks & Richardson 2006). Meerkats teach naïve pups how to handle dangerous food items (Thornton & McAuliffe 2006). Pied babblers, *Turdoides bicolor*, teach offspring a food associated call (Raihani & Ridley 2008). Superb fairy-wrens, *Malurus cyaneus*, teach unhatched young a password call to distinguish them from parasitic cuckoo chicks (Colombelli-Negrel *et al.* 2012; Kleindorfer *et al.* 2014). Zebra finches, *Taeniopygia guttata*, male tutors slow down and exaggerate elements of their songs to teach song to naïve juveniles, similar to infant-directed speech in humans (Chen *et al.* 2016). In this thesis I examined for the first time whether a non-human animal might teach in multiple contexts. Meerkats

clearly have the capacity to teach, so why do they not appear to do so in the context of recognising and responding to SPCs?

Why do meerkats not teach in the context of responses to SPCs?

Teaching occurs in cases when it would be difficult, dangerous, or impossible for individuals to learn asocially or through passive social learning (Thornton & Raihani 2008; Fogarty *et al.* 2011). One possible explanation for the lack of teaching through the mobbing-like response is that learning is not necessary. It is possible that for meerkats recognising and responding to SPCs may be a non-experience dependent behaviour, requiring no learning, and there is consequently no need for adults to promote learning. However, this seems unlikely, given that previous work has shown that responses to alarm calls in meerkats are shaped by experience (Hollén & Manser 2006). Recruitment calls given in response to SPCs, a type of meerkat alarm call, are therefore likely to require learning in how to respond, either socially or asocially. In my work, during experimental cue presentations in 14 out of 18 trials at least one meerkat pup interacted with the predator cues (Chapter two), seeming to follow adults to the recruitment event, touching and sniffing the cues and beginning to perform mobbing-like typical behaviours (personal observation). This, together with the fact that meerkat pups often fail to respond to presentations of cat urine (A Thornton, unpublished data), suggests that there is a role of learning in recognising and responding to SPCs. To investigate whether learning of SPCs is taking place in regards to SPCs, further experimental presentations could be carried out on pups, assessing their responses to SPCs before and after a pairing of the cue with a subsequent predator encounter.

Another potential reason for the lack of evidence for teaching is that the potential benefits of pups learning to respond appropriately may not outweigh the costs of investing in exaggerated responses towards SPCs. Unlike learning to handle dangerous food items (Thornton & McAuliffe 2006), which could have potentially fatal outcomes, learning to recognise predators through SPCs may not provide an unmissable, necessary learning opportunity. While there may be benefits of learning through SPCs this process may not be imperative enough to require promotion by other individuals. The plasticity in response intensity (Chapter two) and frequency (Chapter three) displayed towards SPCs based on current group composition, suggests that responses and possibly information use are variable. By nature

information derived from SPCs is more ambiguous than a direct predator interaction, providing less precise temporal and spatial information about a potential threat. As a result, SPCs may not offer consistent enough information to provide a reliable learning opportunity to justify the costs of teaching.

Finally, while the primary function of the mobbing-like response to SPCs may not be teaching, there may be opportunities for inadvertent social learning. Inadvertent social learning is characterised as the transmission of learnt information between individuals without the need for experienced individuals to adjust their behaviour (Hoppitt *et al.* 2008). Meerkat pups may have sufficient inadvertent learning opportunities through observing knowledgeable group members' high intensity responses to SPCs, without the added need for adults to exaggerate their responses when pups are present. A similar argument can be made for mobbing of actual predators: here, social learning may not be the primary adaptive function, but it can be an additional benefit. For example, captive blackbirds, *Turdus merula*, learnt to mob a harmless novel bird after perceiving a conspecific to be mobbing it (Curio *et al.* 1978a). There is further evidence in naïve juvenile Siberian jays, *Perisoreus infaustus*, which learnt to both recognise and mob a predatory goshawk, *Accipiter gentilis*, following a single observation of a knowledgeable individual mobbing the predator (Griesser & Suzuki 2017). Thus, in a similar way to mobbing of predators, mobbing-like responses towards SPCs may provide sufficient opportunity for inadvertent social learning, negating the need for teaching. Observation of a knowledgeable individual may provide the necessary stimulus enhancement for observational learning to take place. Whether meerkats, and other animals, do learn to recognise and respond to SPCs through observation of others is an area requiring further empirical investigation. This could be achieved by assessing whether there are changes in naïve individuals' responses to SPCs before and after observing a knowledgeable individual interacting with the cue.

Implications for non-human teaching

The lack of evidence for teaching in relation to the mobbing-like response suggests that while meerkats do teach in regards to hunting (Thornton & McAuliffe 2006) they do not teach in this predator-related behaviour. This supports the argument that in non-human animals teaching evolves as a context-specific adaptation, rather being enabled by the evolution of some domain-general cognitive process such as Theory

of Mind (Thornton & Raihani 2008). Indeed, the contrast between limited, context-specific teaching observed in non-human animals compared to the flexible multi-context teaching in humans, is thought to be related to humans' ability to attribute mental states for others (Theory of Mind) as well as the use of language (Thornton & Raihani 2008). This allows humans to communicate knowledge effectively, demonstrate skills, and recognise pupils' current knowledge and adjust their behaviour accordingly. However, it is important to note that the lack of evidence for teaching through the mobbing-like response towards SPCs does not necessarily mean multi-context teaching does not occur outside of humans. While this thesis investigated one possible candidate for multi-context teaching in non-human animals, there may be other as yet unexplored possibilities.

It is possible that the mobbing of live predators may in itself be a form of teaching. If, similar to the predictions I made about the modification of the mobbing-like response to SPCs, knowledgeable individuals increase predator mobbing intensity in the presence of naïve young, then this may be an example of teaching. Given that for a behaviour to be considered a form of teaching, a knowledgeable demonstrator must modify their behaviour to promote learning in a naïve observer at some cost or with no immediate benefit (Caro & Hauser 1992), there is evidence for mobbing meeting parts of these criteria. There is substantial empirical evidence for social learning through mobbing (Curio *et al.* 1978a; Davies & Welbergen 2009; Cornell *et al.* 2012; Griesser & Suzuki 2017). There is also evidence for the costs involved in mobbing responses (time, energy and conspicuousness) that would only be increased by an exaggerated mobbing response (Curio *et al.* 1978b; Krama & Krams 2005; Tórréz *et al.* 2012). Investigating whether adults modify their mobbing response could provide support for predator mobbing playing a role in teaching. Whether adults do exaggerate predator mobbing could be investigated using a similar experimental design as this thesis, assessing changes in adult mobbing intensity dependent on naïve individuals experience levels. If mobbing was found to play a role in teaching, this may provide evidence for non-human animals teaching in multiple contexts. Meerkats and superb fairy-wrens provide prime opportunities to do so, as both are known to mob predators (Graw & Manser 2007; Feeney & Langmore 2013) and show empirical evidence for teaching in other contexts (Thornton & McAuliffe 2006; Colombelli-Negrel *et al.* 2012; Kleindorfer *et al.* 2014).

Potential adaptive functions for the mobbing-like response to SPCs

If mobbing-like responses do not serve as a form of teaching, this raises the question of what their adaptive function may be. Meerkats do appear to use SPCs to inform group defensive behaviours. The recruitment of individuals through this high intensity response may ensure the transfer of threat specific information, more so than may be obtainable from an alarm call, better informing defensive behaviour. While meerkats have a large vocal repertoire, their recruitment calls are thought to only denote threat urgency. Through SPC inspection recruits may be able to acquire detailed personal information not only about the type of predator but also how recently the threat was in the area. Cue specific information about a threat can help prey to tailor their defensive behaviour to the type and severity of threat posed. For example, tadpoles, *Rana temporaria*, show different behavioural responses dependent on which predator cues they are exposed to, varying with predator type and individual vulnerability (Van Buskirk 2001). In larger groups where individuals may be more dispersed, response conspicuousness may be increased to ensure detection and successful information transfer. The results show that in larger group sizes, both mobbing-like response intensity and frequency increased. Meerkats were more likely to interact with the experimental SPC presentation when a greater proportion of the group were recruited (Chapter two), possibly due to a more conspicuous event therefore increasing the probability of information transfer. Larger groups also had a higher rate of natural SPC recruitment events; this may be due to a higher encounter rate in large groups or due to the necessity to transfer information to other group members through SPC inspection (Chapter three). Ensuring that all group members are informed of current risk may be necessary in maintaining the benefit of reduced predation risk through group living, one of the primary benefits conferred (Krause & Ruxton 2002; Caro 2005).

Coordination of group behaviour

The information gathered from SPCs may help to coordinate group defences. One way in which the information may be used is in informing vigilance behaviour. Following an SPC encounter and inspection, one of the most common responses

across many different species is increased vigilance (Belton *et al.* 2007; Furrer & Manser 2009a; Zöttl *et al.* 2013; Mella *et al.* 2014; Garvey *et al.* 2016). This is thought to increase detection of a predator in the vicinity, under the assumption that a SPC is an accurate predictor of increased risk. The increase in alarm calling rate following a natural SPC encounter shown in meerkats suggests that SPCs may be reliable predictors of risk (Chapter three). This is further supported by previous work on meerkats showing an increased detection rate of a predator model following an experimental SPC encounter (Zöttl *et al.* 2013). Thus far this is the only evidence of the increase in vigilance following SPC encounters aiding in predator detection. Although I did not find an increase in raised guarding following a natural SPC encounter, there may have still been an increase in other, more subtle forms of vigilance. For instance, individuals may have increased their own scanning vigilance, which would not have been recorded by current protocols. Under the increased perceived risk it may be more advantageous for multiple individuals to increase investment in anti-predator behaviours (vigilance) rather than relying on a single sentinel (Lima 1987). A greater number of vigilant individuals may have a better chance at detecting a threat. Information from SPCs can help inform where and if vigilance behaviour should be directed. For example, stoats, *Mustela erminea*, responded to predator cues by inspecting them and increasing vigilance, and although they responded more strongly to ferret cues overall they showed greater scanning behaviour to cats which pose above ground than ferrets (Garvey *et al.* 2016). Further study assessing changes in different types of vigilance on both an individual and group level and where this vigilance was directed could provide evidence for how the information derived from SPC encounters is utilised.

The information gathered from SPCs may also help to inform group movement behaviour and aid group cohesion. The reduction in distance travelled following a natural SPC encounter (Chapter three) may indicate either a trade-off with other defensive behaviours, such as vigilance, or the reduction in movement could be part of an adaptive response in itself. The reduction in distance travelled may indicate an increase in group cohesion, facilitated by recruitment to the SPC. The time taken to recruit to and investigate the SPC may have led to the reduction in movement following a SPC encounter. Recruitment to cues may bring the group to a focal point facilitating informed decision making and cohesive movement away. Increasing group cohesion

can help increase survival in the face of predation risk (Mathis & Smith 1993). The increased frequency of SPC recruitment events in larger groups (Chapter three) may also be related to difficulties in maintaining group cohesion in larger groups (Focardi & Pecchioli 2005), necessitating recruitment to SPCs to aid cohesion.

Beyond increasing group-level awareness of the nature of the threat, this recruitment play a role in quorum sensing. Quorum sensing is the process by which animal groups make decisions dependent on a threshold number of individuals performing a particular action (Sumpter & Pratt 2009; Bousquet *et al.* 2011). Many species use quorum sensing in group movement decisions (Pratt & Sumpter 2006; Ward *et al.* 2008; Wolf *et al.* 2013; Walker *et al.* 2017). Quorum decisions can increase both speed and accuracy in group decisions, which is of particular importance in the face of predation risk (Sumpter & Pratt 2009). Previous work has demonstrated that quorum sensing is used by meerkats to induce changes in foraging patch (Bousquet *et al.* 2011). Group movement is achieved following at least two individuals making 'moving' calls signalling unsuccessful foraging and desire to move. In a similar fashion, meerkats may also use quorum sensing when assessing risk indicated by SPCs, recruiting others to corroborate level of risk posed and increase accuracy of appropriate defensive measures. Quorum sensing may be used in deciding whether risk is acute enough to warrant moving away from an otherwise profitable foraging location. Further research is needed to assess whether there are changes in group cohesion following an SPC encounter and whether a threshold of individuals or calls needs to be met to initiate certain defensive responses. Determining how and if there are changes in distance between individuals, and changes in movement direction following a SPC encounter could provide evidence for group cohesion changes.

Social learning

As outlined above, while the mobbing-like response to SPCs does not play a role in teaching, it may still provide valuable opportunities for inadvertent social learning. Social learning using SPCs, outside of learning via conspecific alarm cues in fish (Brown & Godin 1999; Ferrari *et al.* 2006a; Manassa *et al.* 2013; Crane *et al.* 2015), is an area that has received little attention. Yet the benefits of learning using SPCs are potentially great. Given the lack of immediate danger in investigating SPCs, learning through the cues could be advantageous in using them as both indicators of increased

risk, and potentially learning associatively to recognise a live predator. For example, naïve glowlight tetras learn to visually recognise their cichlid predators after exposure and inspection of predator odour containing conspecific alarm pheromones (Brown & Godin 1999). Only inspectors acquired visual recognition of the predator and display antipredator behaviours. Cue inspection facilitated tetras to learn olfactory predator characteristics and associate them with the live threat. Further research is needed into whether other species are able generalise learnt predator recognition from inspecting SPCs, thus providing a substantial survival benefit from a relatively low risk behaviour. By first conditioning a naïve individual to associate a SPC with a threat, it could then be determined whether they are able to generalise this learning to a previously unknown predator or individual.

Mobbing vs the mobbing-like response to SPCs

The mobbing-like response to SPCs in meerkats is almost identical to their mobbing response when encountering a threat. This almost indistinguishable response to SPCs provides a fascinating, possibly unique behaviour, to investigate. Experimental SPC presentations elicited many behaviours typical of a mobbing response: approaching the stimuli, recruitment calls, tail raising, piloerection, and in some cases head bobbing and rocking body movements (Chapter two). This response differed only from predator mobbing in the lack of spit call production, defined in (Graw & Manser 2007). There was also a similar positive effect of group size on frequency of both predator mobbing and mobbing-like response to SPCs (Chapter three). The primary distinction between these two responses is that mobbing is directed at a live predator and the mobbing-like response is not. What the function of the mobbing-like response is, the focus of this thesis, and whether it occurs in other species requires further investigation to disentangle why there are such similarities between the mobbing response to predators and mobbing-like response to SPCs.

Why has this mobbing-like response only been reported in meerkats?

Many animals inspect SPCs (Brown & Godin 1999; Belton *et al.* 2007; Amo *et al.* 2011; Mella *et al.* 2014; Garvey *et al.* 2016), and some also recruit group members to the cues (Furrer & Manser 2009a; Zöttl *et al.* 2013; Collier *et al.* 2017). So why is it that this high intensity mobbing-like response has only been reported in meerkats? A certain degree of sociality is generally associated with alerting conspecifics about

predation risk, thought to be the likely adaptive function of this response, due to the benefits group-living confers (Beauchamp 2013). Species known to share the sociality and SPC inspection characteristics with meerkats are dwarf mongooses, *Helogale parvula*, banded mongooses, *Mungos mungo*, and cape ground squirrels, *Xerus inauris*. These species are all found in Africa with partly overlapping ranges (Manser *et al.* 2014). They are all similar sizes, have similar foraging patterns and subject to similar aerial and terrestrial threats (Furrer & Manser 2009b; Manser *et al.* 2014). They all also mob live predators as a form of defence (Waterman 1997; Graw & Manser 2007; Furrer & Manser 2009a; Kern & Radford 2016). In spite of these similarities there is no reported evidence of a mobbing-like response to SPCs in these species. This may be related to differences in costs of responding unnecessarily to predators, possibly related to differences in habitat.

A potential reason for the lack of evidence, despite the many similarities between meerkats and these other species of mongoose and ground squirrel, may be due to environmental and space use differences. Meerkats primarily forage in very open, semi-arid habitats, whereas both dwarf and banded mongooses live in vegetated areas (Manser *et al.* 2014). Vegetated habitats may provide greater and more accessible shelter opportunities following indication of a potential predator in the vicinity. Furthermore, a more-vegetated environment may hamper the ability to visually detect a predator following a SPC encounter, making it more adaptive to respond quickly rather than further assessing risk. In contrast, meerkats' open foraging habitats results in greater distances to shelter, potentially making the cost of ceasing foraging to seek shelter greater without first assessing severity of risk. While cape ground squirrels live sympatrically with meerkats in open habitats, they forage much closer to their burrows, remaining in closer proximity to shelter (Furrer & Manser 2009b). As a result it is again less costly for cape ground squirrels to respond defensively and flee in the face of potentially increased risk. These suggested differences in habitat and space use by meerkats and the other mongoose and squirrel species, are also thought to be possible drivers of differences in their alarm call systems (Furrer & Manser 2009b; Manser *et al.* 2014).

Another potential candidate that shares similar sociality and habitat conditions are pied babblers. These birds also live sympatrically with meerkats, are cooperative breeders,

range widely while foraging in open habitats, and are under high predation risk from similar threats (Ridley 2016). While there is only one reported example of SPC inspection in birds (Amo *et al.* 2011), and no evidence for recruitment to SPCs, this does not necessarily mean that it does not occur. American crows, *Corvus brachyrhynchos*, and Western scrub-jays, *Aphelocoma californica*, aggregate and mob the bodies of dead conspecifics (Iglesias *et al.* 2012; Swift & Marzluff 2015). The function of this recruitment and response is unclear. The birds may be able to detect and inspect cues left on dead conspecifics by a predator, such as saliva or other scents, using these to learn the source of the threat. Further study is needed into firstly, whether other avian species detect and respond to SPCs. Secondly, whether SPCs can be used in this context to learn about risks, particularly through a mobbing-like response.

Conclusions

Gaining an understanding of the possibly unique mobbing-like response to SPCs will provide insight into how, when and why these cues are used to inform behaviour. The lack of teaching in this context also provides further evidence for a potential key difference in human and non-human animal teaching. The more general role of learning both in SPC recognition and generalisation of this learning to predators is a vital one to be explored to highlight substantial benefits of utilising information from these cues. The field of studying SPCs is varied, spanning many disciplines from evolutionary biology, neurology, conservation, behavioural ecology and chemistry. Much of the research into SPCs focuses on the morphological and physiological changes in phenotypes resulting from SPC exposure and, in terms of behavioural responses, focuses predominately on whether or not there is a response. Little attention is given to how these behavioural responses actually benefit prey in successfully evading predators and the processes by which these responses are developed. Only by gaining a greater understanding of the significance and fitness benefits of SPCs in informing behaviour will we fully understand how information from different stimuli can shape prey phenotypes.

Appendix 1. – Supplementary material for Chapter Two

As the number of pups in the NP treatment was, by definition, zero, the effects of treatment and number of pups could be correlated. To address this, we also ran the analysis with the results of the NP treatment excluded. The results of these models were qualitatively very similar to those conducted on the full dataset (Table 1).

Table 1 – Table showing the models in the top set for each aspect of response intensity, comparing the full data set with that of the dataset with the NP treatment excluded. Top models highlighted in bold following application of the nesting rule. Asterix signifies a significant effect and “NS” indicates non-significant.

All conditions				Without NP			
(a) Proportion recruited							
Model	AIC	Fixed effects	Significant?	Model	AIC	Fixed effects	Significant?
a.5	127.64	No. pups	*	a.4	94.05	Call type	*
a.6	129.26	No. pups	*	a.6	95.5	No. pups	NS
		Call type	NS			Call type	*
(b) Interact (y/n)							
Model	AIC	Fixed effects	Significant?	Model	AIC	Fixed effects	Significant?
b.10	236.71	Prop. recruited	*	b.10	176.38	Prop. recruited	*
b.9	239.06	Prop. recruited	*	b.9	179.27	Prop. recruited	*
		Call type	NS			Call type	NS
b.11	240.4	Prop. recruited	*	b.11	179.36	Prop. recruited	*
		Treatment	NS			Treatment	NS
(c) Interact duration							
Model	AIC	Fixed effects	Significant?	Model	AIC	Fixed effects	Significant?
c.5	801.22	Cue type	*	c.6	553.3	Treatment	*
c.6	803.3	Cue type	*			Cue type	*
		Treatment	NS	c.5	554.9	Cue type	*
c.7	806.1	Treatment	*	c.3	558.5	Treatment	*
		No. pups	*			No. pups	NS
(d) Tail raised (y/n)							
Model	AIC	Fixed effects	Significant?	Model	AIC	Fixed effects	Significant?
d.13	66.3	No. adults	*	d.9	55.47	Call type	*
		No. pups	*			Prop. recruited	NS

d.4	68.15	No. pups	*	d.7	56.38	Call type	*
d.7	68.99	Call type	*	d.10	59.78	Prop. recruited	NS
(e) Tail raised duration							
Model	AIC	Fixed effects	Significant?	Model	AIC	Fixed effects	Significant?
e.4	481.73	No. pups	*	e.13	299.31	No. pups	*
e.13	484.04	No. pups	*			No. adults	*
		No. adults	NS	e.5	300.21	Cue type	*
e.3	486.93	No. pups	*	e.4	303.29	No. pups	NS
		Treatment	NS				
(f) Piloerect (y/n)							
Model	AIC	Fixed effects	Significant?	Model	AIC	Fixed effects	Significant?
f.5	93.23	Cue type	*	f.10	65.9	Prop. recruited	*
f.10	94	Prop. recruited	*	f.5	67.6	Cue type	*
f.11	96.9	Prop. recruited	*	f.11	68.4	Prop. recruited	*
		Treatment	NS			Treatment	NS
(g) Piloerect duration							
Model	AIC	Fixed effects	Significant?	Model	AIC	Fixed effects	Significant?
g.13	288.3	No. adults	*	g.12	166.6	No. adults	*
		No. pups	*	g.13	170.07	No. adults	*
g.2	292.8	Treatment	*			No. pups	NS
g.12	292.9	No. adults	*				

Table 1 shows that the models forming the top set were broadly consistent between the full dataset and that with the NP treatment excluded. The models in the top set for the NP-excluded dataset differ primarily only for the proportion of the group recruited, whether individuals raised their tails and piloerection duration. For these indicators of response intensity for the full dataset the number of pups had an effect, whereas when the NP treatment is excluded the numbers of pups did not have an effect. This may suggest that it is the presence of pups alone rather than the increasing number that drives this effect in the full dataset. There remains a negative effect of pup number for tail raised duration in both the full dataset and the NP-excluded data.

Table 2. – Model summaries of the top candidate models for the indicators of mobbing intensity. (a) The proportion of the group recruited to predator cue presentation. (b) Whether an individual interacted with the cue. (c) The duration of an individual's interaction. (d) Whether an individual raised their tail. (e) The duration an individual raised their tail for. (f) Whether an individual piloerected. (g) The duration an individual piloerected for.

	Estimate	Standard Error	z value	Pr(> z)	
a. Proportion recruited					
<i>Number of Pups</i>					
(Intercept)	-0.0502	0.3151	-0.159	0.8733	
No. pups	-0.2009	0.1066	-1.884	0.0595	.
b. Interact y/n					
<i>Proportion Recruited</i>					
(Intercept)	-1.2605	0.2685	-4.694	2.68E-06	***
Prop. Recruited	2.9917	0.8166	3.664	0.000249	***
c. Interact duration					
<i>Cue Type</i>					
(Intercept)	3.5041	0.1394	25.139	1.87E-139	***
Fur	0	0			
Urine	-0.5112	0.1690	-3.025	0.002486	**
d. Raised tail y/n					
<i>(d.4) Number of Pups</i>					
(Intercept)	3.2355	0.8295	3.900	9.6e-05	***
No. Pups	-0.6913	0.2430	-2.844	0.00445	**
<i>(d.7) Recruitment call type</i>					
(Intercept)	0.5465	0.3789	1.443	0.14914	
High	2.3979	0.8184	2.930	0.00339	**
Target	-0.5465	1.4641	-0.373	0.70892	
e. Tail raised duration					
<i>Number of Pups</i>					
(Intercept)	0.0820	0.0205	4.000	6.35E-05	***
No. Pups	0.0158	0.0042	3.799	0.000145	***
f. Piloerect y/n					
<i>(f.5) Cue Type</i>					
(Intercept)	-1.8295	0.8608	-2.126	0.033544	**
Fur	0	0			
Urine	2.3331	0.7007	3.330	0.000870	**
<i>(f.10) Proportion Recruited</i>					
(Intercept)	0.6112	1.0091	0.606	0.544714	
Prop. Recruited	-5.3586	1.7668	-3.033	0.002422	**

g. Piloerection duration*(g.13) Number of Adults + Number of Pups*

(Intercept)	1.5714	0.4709	3.337	0.000847	***
No. adults	0.1233	0.0384	3.212	0.001319	**
No. pups	-0.1890	0.0598	-3.161	0.001573	**

(g.2) Treatment

(Intercept)	3.2161	0.2800	11.487	< 2e-16	***
PP1	-0.8084	0.1922	-4.206	2.60e-05	***
PP2	-1.1039	0.3016	-3.660	0.000252	***
PP3	-1.1123	0.2663	-4.177	2.96e-05	***

a. Proportion of group recruited

Table 3. – Model selection table for the variables affecting the proportion of the adults in the group recruited to the predator cue presentation ranked by AIC value. Variables tested are the recruitment call category (high, low/none, individual presented to), treatment (NP, PP1, PP2, PP3), cue type (fur, urine), number of adults in the group, number of pups in the group. Retained models in bold.

Model	Fixed Effects	Intercept	Call Type	Treatment	Cue Type	No. Adults	No. Pups	df	logLik	AICc	delta	weight
a.5	No. Pups	-0.050					-0.201	3	-60.221	127.64	0.00	0.463
a.6	No. Pup +Call Type	-0.226			+		-0.215	4	-59.591	129.29	1.65	0.203
a.3	Treatment	-0.275		+				3	-61.577	130.35	2.71	0.119
a.4	Cue Type	-0.588			+			3	-61.904	131.01	3.37	0.086
a.7	No. Adults	-0.250				-0.020		3	-62.053	131.31	3.67	0.074
a.2	Call Type	-0.051	+					5	-59.296	131.93	4.28	0.054
a.1	ALL	-0.269	+	+	+	0.024	-0.275	9	-57.835	146.53	18.88	0.000

b. Interact (y/n)

Table 4. – Model selection table for the variables affecting whether an individual interacts with the predator cue presentation ranked by AIC value. Variables tested are the recruitment call category (high, low, none, individual presented to), treatment (NP, PP1, PP2, PP3), cue type (fur, urine), number of adults in the group, number of pups in the group, proportion of the group interacting with the cue. Retained models in bold.

Model	Fixed Effects	Intercept	Call Type	Treatment	Cue Type	No. Adults	No. Pups	Prop Interact	df	logLik	AICc	delta	weight
b.10	Prop Recruit	-1.260						2.992	4	-114.245	236.71	0.00	0.665
b.9	Call Type + Prop Recruit	-1.233	+					2.695	6	-113.292	239.06	2.35	0.206
b.11	Prop Recruit + Treatment	-0.878		+				2.722	7	-112.879	240.40	3.68	0.105

b.1	ALL	-1.034	+	+	+	0.055	-0.429	2.056	12	-109.412	244.66	7.95	0.013
b.4	No. Pups	-0.048					-0.217		4	-119.541	247.31	10.59	0.003
b.7	Call Type	-0.545	+						5	-118.845	248.03	11.32	0.002
b.13	No. Adults + No. Pups	-0.427				0.040	-0.223		5	-119.321	248.98	12.27	0.001
b.2	Treatment	-0.042		+					6	-118.536	249.55	12.83	0.001
b.8	Call Type + Treatment	-0.106	+	+					8	-116.473	249.77	13.06	0.001
b.3	Treatment + No. Pups	-0.082		+			-0.245		7	-117.920	250.48	13.76	0.001
b.5	Cue Type	-0.317			+				4	-121.150	250.52	13.81	0.001
b.6	Cue Type + Treatment	0.119		+	+				7	-118.226	251.09	14.38	0.001
b.12	No. Adults	-0.662				0.017			4	-121.564	251.35	14.64	0.000

c. Interact duration

Table 5. – Model selection table for the variables affecting whether an individual's interaction duration with the predator cue presentation ranked by AIC value. Variables tested are the recruitment call category (high, low, none, individual presented to), treatment (NP, PP1, PP2, PP3), cue type (fur, urine), number of adults in the group, number of pups in the group, proportion of the group interacting with the cue. Retained models in bold.

Model	Fixed Effects	Intercept	Call Type	Treatment	Cue Type	No. Adults	No. Pups	Prop Recruit	df	logLik	AICc	delta	weight
c.5	Cue Type	3.504			+				5	-395.263	801.22	0.00	0.622
c.6	Cue Type + Treatment	3.659		+	+				8	-392.781	803.30	2.07	0.221
c.3	Treatment + No. Pups	3.398		+			0.243		8	-394.207	806.15	4.93	0.053
c.7	Call Type	3.496	+						7	-396.125	807.58	6.36	0.026
c.12	No. Adults	3.612				-0.037			5	-398.898	808.49	7.27	0.016
c.2	Treatment	3.346		+					7	-396.785	808.90	7.68	0.013
c.1	ALL	3.997	+	+	+	-0.040	0.182	-0.526	14	-388.174	809.80	8.58	0.009

c.9	Call Type + Prop Recruit	3.508	+			-0.051	8	-396.118	809.97	8.75	0.008
c.10	Prop Recruit	3.264				-0.051	5	-399.648	809.99	8.77	0.008
c.4	No. Pups	3.245			0.005		5	-399.652	810.00	8.78	0.008
c.8	Call Type + Treatment	3.638	+	+			10	-393.862	810.44	9.22	0.006
c.13	No. Adults + No. Pups	3.590			-0.037	0.018	6	-398.848	810.68	9.46	0.005
c.11	Prop Recruit + Treatment	3.393		+			8	-396.650	811.03	9.81	0.005

Table 6. – Model summaries of the GLMM's containing condition forming the top set for interaction duration.

	Estimate	Std. Error	t value	Pr(> z)
<i>c.6 Treatment & Cue type</i>				
(Intercept)	3.6587	0.2015	18.160	1.07E-73
CueTypeUrine	-0.4993	0.1716	-2.910	0.0036
TreatmentPP1	-0.2484	0.2275	-1.092	0.2749
TreatmentPP2	-0.5488	0.2507	-2.189	0.0286
TreatmentPP3	-0.1338	0.2140	-0.625	0.5319
<i>c.3 Treatment & Number of pups</i>				
(Intercept)	3.3981	0.1673	20.311	1.02E-91
TreatmentPP1	-0.7826	0.3508	-2.231	0.0257
TreatmentPP2	-1.4774	0.4749	-3.111	0.0019
TreatmentPP3	-0.8329	0.4222	-1.973	0.0485
NumPups	0.2432	0.1065	2.283	0.0224

d. Tail raised (y/n)

Table 7. – Model selection table for the variables affecting whether an individual raises their tail while interacting with the predator cue presentation ranked by AIC value. Variables tested are the recruitment call category (high, low/none, individual presented to), treatment (NP, PP1, PP2, PP3), cue type (fur, urine), number of adults in the group, number of pups in the group, proportion of the group interacting with the cue. Retained models in bold.

Model	Fixed Effects	Intercept	Call Type	Treatment	Cue Type	No. Adults	No. Pups	Prop Recruit	df	logLik	AICc	delta	weight
d.13	No. Adults + No. Pups	0.777				0.324	-0.985		5	-27.732	66.37	0.00	0.456
d.4	No. Pups	3.235					-0.691		4	-29.779	68.15	1.78	0.187
d.7	Call Type	2.944	+						5	-29.042	68.99	2.62	0.123
d.8	Call Type + Treatment	5.002	+	+					8	-25.502	69.29	2.92	0.106
d.9	Call Type + Prop Recruit	3.367	+					-1.350	6	-28.605	70.50	4.13	0.058
d.1	ALL	3.742	+	+	+	0.779	-0.831	-4.179	12	-21.068	71.42	5.05	0.036
d.3	Treatment + No. Pups	2.996		+			-0.753		7	-29.319	74.39	8.01	0.008
d.11	Prop Recruit + Treatment	5.375		+				-2.915	7	-29.543	74.84	8.46	0.007
d.10	Prop Recruit	2.396						-1.744	4	-33.239	75.08	8.70	0.006
d.2	Treatment	3.569		+					6	-30.946	75.18	8.81	0.006
d.12	No. Adults	1.069				0.072			4	-33.895	76.39	10.01	0.003
d.5	Cue Type	1.847			+				4	-33.978	76.55	10.18	0.003
d.6	Cue Type + Condition	4.131		+	+				7	-30.808	77.37	10.99	0.002

e. Tail raised duration

Table 8. – Model selection table for the variables affecting the duration an individual’s tail is raised for during an interaction with the predator cue presentation ranked by AIC value. Variables tested are the recruitment call category (high, low/none, individual presented to), treatment (NP, PP1, PP2, PP3), cue type (fur, urine), number of adults in the group, number of pups in the group, proportion of the group interacting with the cue. Retained models in bold.

Model	Fixed Effects	Intercept	Call Type	Treatment	Cue Type	No. Adults	No. Pups	Prop Recruit	df	logLik	AICc	delta	weight
e.4	No. Pups	0.082					0.016		5	-235.395	481.73	0.00	0.668
e.13	No. Adults + No. Pups	0.096				-0.001	0.015		6	-235.352	484.04	2.31	0.210
e.3	Treatment + No. Pups	0.090		+			0.032		8	-234.285	486.93	5.20	0.050
e.6	Cue Type + Treatment	0.102		+	+				8	-235.457	489.27	7.55	0.015
e.8	Call Type + Treatment	0.057	+	+					9	-234.170	489.34	7.61	0.015
e.5	Cue Type	0.132			+				5	-239.477	489.89	8.16	0.011
e.2	Treatment	0.078		+					7	-237.067	489.94	8.21	0.011
e.12	No. Adults	0.170				-0.007			5	-239.685	490.31	8.58	0.009
e.11	Prop Recruit + Treatment	0.071		+				0.027	8	-236.702	491.76	10.04	0.004
e.1	ALL	0.142	+	+	+	-0.006	0.028	0.052	13	-229.655	491.81	10.08	0.004
e.7	Call Type	0.080	+						6	-240.654	494.64	12.91	0.001
e.9	Call Type + Prop Recruit	0.072	+					0.028	7	-240.472	496.75	15.02	0.000
e.10	Prop Recruit	0.095						0.017	5	-243.365	497.67	15.94	0.000

f. Piloerection (y/n)

Table 9. – Model selection table for the variables affecting whether an individual piloerects during an interaction with the predator cue presentation ranked by AIC value. Variables tested are the treatment (NP, PP1, PP2, PP3), cue type (fur, urine), number of adults in the group, number of pups in the group, proportion of the group interacting with the cue. Models containing recruitment call category were not included because of convergence issues due to no individuals piloerecting for the low/none category. Retained models in bold.

Model	Fixed Effects	Intercept	Treatment	Cue Type	No. Ad	No. Pups	Prop Recruit	df	logLik	AICc	delta	weight
f.1	ALL	-1.669	+	+	0.147	-1.991	-9.050	10	-28.695	80.11	0.00	0.997
f.5	Cue Type	-1.830		+				4	-42.387	93.23	13.13	0.001
f.10	Prop Recruit	0.611					-5.359	4	-42.768	94.00	13.89	0.001
f.11	Prop Recruit + Treatment	1.157	+				-5.949	7	-40.810	96.95	16.85	0.000
f.6	Cue Type + Treatment	-1.721	+	+				7	-41.945	99.22	19.12	0.000
f.4	NumPups	0.054				-0.323		4	-47.695	103.85	23.74	0.000
f.13	No. Ad + No. Pups	-1.227			0.144	-0.327		5	-47.181	105.06	24.95	0.000
f.3	Treatment + No. Pups	-0.335	+			-0.970		7	-45.130	105.59	25.49	0.000
f.12	No. Ad	-1.953			0.157			4	-48.573	105.61	25.50	0.000
f.2	Condition	-0.168	+					6	-47.592	108.17	28.07	0.000

g. Piloerection duration

Table 10. – Model selection table for the variables affecting the duration an individual piloerected for during an interaction with the predator cue presentation ranked by AIC value. Variables tested are the recruitment call category (high, low/none, individual presented to), treatment (NP, PP1, PP2, PP3), cue type (fur, urine), number of adults in the group, number of pups in the group, proportion of the group interacting with the cue. Retained models in bold.

Model	Fixed Effects	Intercept	Call Type	Treatment	Cue Type	No. Adults	No. Pups	Prop Recruit	df	logLik	AICc	delta	weight
g.13	No. Adults + No. Pups	1.571				0.123	-0.189		6	-136.784	288.28	0.00	0.731
g.2	Treatment	3.216		+					7	-137.569	292.87	4.59	0.074
g.12	No. Adults	0.582				0.206			5	-140.528	292.93	4.65	0.071
g.4	No. Pups	2.906					-0.251		5	-141.028	293.93	5.65	0.043
g.6	Cue Type + Treatment	3.003		+	+				8	-137.064	295.09	6.81	0.024
g.11	Prop Recruit + Treatment	3.383		+				-0.762	8	-137.208	295.38	7.10	0.021
g.8	Call Type + Treatment	3.298	+	+					8	-137.269	295.50	7.22	0.020
g.3	Condition + No. Pups	3.241		+			0.037		8	-137.532	296.03	7.75	0.015
g.10	Prop Recruit	2.912						-1.122	5	-145.709	303.29	15.01	0.000
g.9	Call Type + Prop Recruit	3.450	+					-2.365	6	-144.751	304.21	15.93	0.000
g.1	ALL	2.368	+	+	+	0.082	-0.060	-1.375	12	-134.164	304.81	16.53	0.000
g.5	Cue Type	2.539			+				5	-146.553	304.98	16.70	0.000
g.7	Call Type	2.648	+						5	-146.653	305.18	16.90	0.000

Table 11. – Model summaries of the GLMM's containing treatment forming the top set for piloerection duration.

	Estimate	Std. Error	t value	Pr(> z)
<i>g.2 Treatment</i>				
(Intercept)	3.2161	0.2800	11.487	< 0.001
TreatmentPP1	-0.8084	0.1922	-4.206	< 0.001
TreatmentPP2	-1.1039	0.3016	-3.660	< 0.001
TreatmentPP3	-1.1123	0.2663	-4.177	< 0.001

Appendix 2. – Supplementary material for Chapter Three

Recruitment event rate

Table 1. – Model summaries of the top candidate models using AIC model selection for predicting frequency of recruitment event to (a) secondary predator cues and (b) animals.

	Estimate	Std Error	df	ChiSq	
a. Secondary predator cue					
(a13) Proportion of pups* Average group size					
Intercept	0.6836	0.0861			
Prop. pups	-0.2330	0.5090	1	< 0.001	***
Group size	0.0459	0.0047	1	< 0.001	***
Prop. pups:Group size	-0.0638	0.0369	1	0.08387	
(a12) Pups foraging (y/n)* Average group size					
Intercept	0.6888	0.0870			
Forage	-0.2873	0.1488	1	< 0.001	***
Group size	0.0458	0.0048	1	< 0.001	***
Forage:Group size	-0.0006	0.0082	1	0.9444	
b. Animal					
(b6) Average group size					
Intercept	0.3105	0.0516			
Group size	0.0251	0.0029	1	< 0.001	***
(b13) Proportion of pups* Average group size					
Intercept	0.3249	0.0542			
Prop. pups	-0.2232	0.3879	1	0.09245	
Group size	0.0252	0.0031	1	< 0.001	***
Prop. pups:Group size	-0.0045	0.0280	1	0.8733	
(b12) Pups foraging (y/n)* Average group size					
Intercept	0.3165	0.0552			
Forage	-0.0444	0.1133	1	0.4355	
Group size	0.0252	0.0032	1	< 0.001	***
Forage:Group size	0.0005	0.0062	1	0.9396	

a. Secondary predator cue rate

Table 2 – Model selection table for the factors affecting frequency of SPC recruitment events ranked by AIC value. Variables tested are pups foraging with the group (y/n), previous 30 day total rainfall, previous 9 month total rainfall, previous 30 days average maximum daily temperature, proportion of females in the group, proportion of pups in the group. Models forming the top set in bold.

	Intercept	Forage	Rainfall 30Days	Rainfall 9Months	MaxTemp 30Days	Prop F	Group Size	Prop Pups	Forage: Rainfall 30Days	Forage: Rainfall 9Months	Forage: MaxTemp 30Days	Forage: PropF	GroupSize: Forage	GroupSize: PropPups	MaxTemp 30Days: Rainfall 30Days	MaxTemp 30Days: Rainfall 9Months	MaxTemp 30Days: Rainfall 9Months	df	loglik	AICc	delta	weight
a13	0.68						0.05	-0.23						-0.06				7	-5022.91	10059.87	0.00	0.76
a12	0.69	+					0.05					+						7	-5024.07	10062.18	2.32	0.24
a6	0.66						0.04											5	-5035.55	10081.12	21.25	0.00
a14	-0.93		9.43	0.05											-0.23			7	-5038.13	10090.29	30.42	0.00
a9	0.87	+	2.26						+									7	-5044.91	10103.86	44.00	0.00
a3	0.86		2.11															5	-5051.62	10113.27	53.40	0.00
a15	1.74		11.65		-0.02										-0.24			7	-5060.61	10135.27	75.40	0.00
a8	1.25	+	3.26					+										7	-5062.77	10139.59	79.72	0.00
a7	1.32						-1.01											5	-5067.36	10144.74	84.87	0.00
a11	1.61	+				-0.64						+						7	-5067.33	10148.69	88.83	0.00
a10	1.65	+			-0.01					+								7	-5068.04	10150.13	90.26	0.00
a2	1.20		2.79															5	-5070.75	10151.51	91.65	0.00
a1	1.31	+																5	-5071.05	10152.13	92.26	0.00
a4	1.65				-0.01													5	-5073.72	10157.45	97.59	0.00
a5	1.50					-0.50												5	-5075.59	10161.21	101.34	0.00

b. Animal mobbing rate

Table 3 – Model selection table for the factors affecting frequency of animal recruitment events ranked by AIC value. Variables tested are pups foraging with the group (y/n), previous 30 day total rainfall, previous 9 month total rainfall, previous 30 days average maximum daily temperature, proportion of females in the group, proportion of pups in the group. Models forming the top set in bold.

	Intercept	Forage	Rainfall 30DaysL	Rainfall 9Months	MaxTemp 30Days	Prop F	Group size	PropPups	Forage:Rainfall 30Days	Forage:Rainfall 9Months	Forage:MaxTemp 30Days	Forage:Prop F	Group Size:Forage	GroupSize:Prop pups	MaxTemp 30Days:Rainfall 9Months	MaxTemp 30Days:Rainfall 30Days	df	logLik	AICc	delta	weight
b6	0.31						0.03										5	-4233.86	8477.73	0.00	0.57
b13	0.32						0.03	-0.22						0.00			7	-4232.43	8478.89	1.16	0.32
b12	0.32	+					0.03						+				7	-4233.55	8481.14	3.40	0.10
b4	0.27				0.01												5	-4260.09	8530.20	52.47	0.00
b14	-0.21			2.10	0.03										-0.06		7	-4258.27	8530.57	52.84	0.00
b10	0.34	+			0.01						+						7	-4258.83	8531.70	53.97	0.00
b15	0.34		-3.61		0.01											0.13	7	-4258.96	8531.95	54.22	0.00
b2	0.65		1.44														5	-4264.72	8539.46	61.73	0.00
b8	0.64	+	1.87						+								7	-4263.93	8541.90	64.16	0.00
b7	0.70							-0.29									5	-4266.42	8542.86	65.12	0.00
b5	0.82					-0.29											5	-4266.47	8542.95	65.22	0.00
b3	0.74			-													5	-4266.72	8543.46	65.72	0.00
				0.33																	
b9	0.72	+		-						+							7	-4265.79	8545.62	67.89	0.00
				0.20																	
b1	0.68	+															5	-4267.93	8545.88	68.14	0.00
b11	0.79	+				-0.23						+					7	-4265.96	8545.97	68.23	0.00

Behavioural changes following recruitment event

Table 4. – Model summaries of the top candidate models following AIC model selection for various behaviours that may change following a SPC recruitment event; (c) alarm calling rate, (d) guarding rate, (f) distance travelled, (e) per pup provisioning rate.

	Estimate	Std Error	df	ChiSq	
c. Alarm calling rate					
(c8) Hour before or after*Daily maximum temperature					
Intercept	1.247	0.084			
Before/after	0.033	0.110	1	< 0.001	***
Max. Temp.	-0.015	0.003	1	< 0.001	***
Before or after:Max. temp.	-0.004	0.004	1	0.269	
(c12) Daily maximum temperature*Rainfall 9 Months					
Intercept	1.567	0.162			
Max. Temp.	-0.028	0.005	1	< 0.001	***
Rainfall 9 Months	-1.432	0.582	1	0.342	
Max. Temp.*Rainfall 9 Months	0.054	0.019	1	0.004	**
d. Guarding rate					
(d18) Pups foraging (y/n)*Rainfall 9 Months					
Intercept	-0.200	0.071			
Forage	0.351	0.087	1	< 0.001	***
Rainfall 9 Months	2.748	0.206	1	< 0.001	***
Forage*Rainfall 9 Months	-0.847	0.331	1	0.011	*
e. Distance travelled					
(e8) Hour before or after*Max. temp.					
Intercept	4.481	0.087			
Before/after	0.268	0.116	1	< 0.001	***
Max. temp.	0.019	0.003	1	< 0.001	***
Before/after *Max. temp.	-0.005	0.004	1	0.146	
(e12) Daily maximum temperature*Rainfall 9 Months					
Intercept	4.668	0.164			
Max. temp.	0.019	0.005	1	< 0.001	***
Rainfall 9 Months	0.343	0.658	1	< 0.001	***
Max. temp.*Rainfall 9 Months	-0.033	0.021	1	0.116	
(e13) Daily maximum temperature *Rainfall 30 days					

Intercept	4.526	0.075			
Max. Temp.	0.020	0.002	1	< 0.001	***
Rainfall 30 days	4.079	2.608	1	0.001	***
Max. temp.*Rainfall 30 Days	-0.170	0.080	1	0.034	*

f. Per pup provisioning rate

(f14) Proportion of pups

Intercept	0.322	0.233			
Prop. pups	-2.864	0.626	1	< 0.001	***

(f15) Proportion of pups*Average group size

Intercept	0.160	0.458			
Prop. pups	-0.793	1.441	1	< 0.001	***
Group size	0.013	0.018	1	0.264	
Prop. pups*Group size	-0.147	0.076	1	0.057	

(f3) Proportion of pups*Hour before or after

Intercept	0.289	0.248			
Prop. pups	-2.785	0.729	1	< 0.001	***
Before/after	0.065	0.170	1	0.629	
Prop. pups* Before/after	-0.154	0.762	1	0.840	

c. Alarm calling rate

Table 5 – Model selection table for the factors affecting hourly alarm calling rate ranked by AIC value. Variables tested are the hour before or after a recruitment event, pups foraging with the group (y/n), proportion of pups in the group, predator cue type (scent or object), previous 30 day total rainfall, previous 9 month total rainfall, daily maximum temperature. Models forming the top set in bold.

Model	Intercept	B/A	Forage	B/A:Forage	Pred Code	B/A:PredCode	PropPups	B/A:PropPups	GroupSize	B/A:GroupSize	Rainfall9MonthsL	B/A:Rainfall 9Months	Rainfall30Days	AlarmFac:Rainfall	MaxTemp	B/A:MaxTemp	MaxTemp:Rainfall9Mont	MaxTemp:Rainfall9Mont	GroupSize:PropPups	MaxTemp:Rainfall	Forage:PredCode	Forage:MaxTemp	Forage:Rainfall 9Months	Forage:Rainfall 30Days	Forage:GroupSize	df	logLik	AIC	delta	weight
c8	1.2	+														+										7	-	27224.	0.00	0.92
	5														0.0												13605.	28		
															1												14			
c1	1.5										-						0.0									7	-	27229.	5.58	0.06
2	7										1.4						5										13607.	86		
											3																93			
c1	1.3												-				0.1									7	-	27232.	8.06	0.02
3	5												4.7				6										13609.	34		
													1														17			
c2	1.2																									5	-	27234.	10.5	0.00
2	6																										13612.	85	7	
																											42			
c1	1.2	+																			+					7	-	27236.	11.8	0.00
8	2																										13611.	16	8	
																											08			
c6	0.6	+									0.8	+														7	-	27270.	46.5	0.00
	2										4																13628.	87	9	
																											43			
c1	0.6										0.7															5	-	27280.	56.0	0.00
1	0										4																13635.	34	6	
																											17			

c1 9	0.6 2	+			0.7 2			+	7	- 13633. 58	27281. 16	56.8 8	0.00
c2	0.8 1	+	+	+					7	- 13639. 13	27292. 26	67.9 8	0.00
c4	0.7 9	+			0.3 8	+			7	- 13639. 20	27292. 40	68.1 2	0.00
c1	0.8 1	+							5	- 13642. 55	27295. 11	70.8 3	0.00
c5	0.7 7	+			0.0 0	+			7	- 13641. 15	27296. 30	72.0 2	0.00
c7	0.8 1	+					- 0.2 6	+	7	- 13641. 28	27296. 57	72.2 9	0.00
c3	0.7 9	+		+	+				7	- 13642. 50	27298. 99	74.7 1	0.00
c1 6	0.7 4				1.0 0	0.0 0			7	- 13644. 65	27303. 29	79.0 1	0.00
c1 4	0.7 8	+							5	- 13647. 18	27304. 35	80.0 7	0.00
c2 1	0.7 6	+			0.0 0				7	- 13645. 93	27305. 86	81.5 8	0.00
c2 3	0.7 8						- 0.4 8		5	- 13647. 95	27305. 90	81.6 2	0.00
c2 0	0.7 9	+					- 0.4 9		7	- 13646. 38	27306. 77	82.4 9	0.00

d1	-			2.5					5	-	24529.	18.7	0.0
0	0.1			1						12259.	12	9	0
	0									56			
d1	0.1			1.3				0.04	7	-	24530.	20.2	0.0
1	7			7						12258.	54	1	0
										26			
d1	0.9	+							7	-	24634.	124.	0.0
7	7									12310.	66	33	0
										32			
d2	0.9								5	-	24649.	139.	0.0
1	7									12319.	40	08	0
										70			
d1	1.0			-				0.03	7	-	24651.	141.	0.0
2	0			0.3						12318.	97	64	0
				4						98			
d8	0.9	+							7	-	24653.	142.	0.0
	3									12319.	06	74	0
										52			
d1	0.1		0.9	0.0				0.0	7	-	24658.	147.	0.0
5	7		4	1				0		12322.	30	97	0
										14			
d1	0.4		0.9						5	-	24668.	158.	0.0
4	0		5							12329.	71	39	0
										35			
d2	0.1	+		0.0					7	-	24671.	160.	0.0
0	4			2						12328.	12	79	0
										55			
d4	0.3	+	1.0	+					7	-	24671.	161.	0.0
	8		9							12328.	83	50	0
										91			
d5	0.1	+		0.0	+				7	-	24675.	165.	0.0
	0			2						12330.	73	40	0
										86			
d9	0.2			0.0					5	-	24678.	168.	0.0
	0			1						12334.	90	57	0
										44			

d1 6	0.2 7		+						+		7	- 12333. 63	24681. 28	170. 95	0.0 0
d1 3	0.4 1		+								5	- 12337. 02	24684. 05	173. 73	0.0 0
d1 9	0.4 1		+			- 0.2 5				+	7	- 12336. 42	24686. 85	176. 52	0.0 0
d2	0.3 9	+	+	+							7	- 12336. 60	24687. 22	176. 90	0.0 0
d8	0.3 3							+			5	- 12339. 80	24689. 62	179. 29	0.0 0
d3	0.3 4	+						+	+		7	- 12339. 70	24693. 41	183. 09	0.0 0
d2 2	0.4 5					- 0.2 8					5	- 12342. 43	24694. 86	184. 53	0.0 0
d1	0.4 4	+									5	- 12342. 59	24695. 19	184. 86	0.0 0
d7	0.4 5	+				- 0.5 0			+		7	- 12342. 22	24698. 46	188. 14	0.0 0

e. Distance travelled

Table 7 – Model selection table for the factors distance travelled in an hour ranked by AIC value. Variables tested are the hour before or after a recruitment event, pups foraging with the group (y/n), proportion of pups in the group, predator cue type (scent or object), previous 30 day total rainfall, previous 9 month total rainfall, daily maximum temperature. Models forming the top set in bold.

	Intercept	B/A	Forage	B/A:Forage	PredCode	B/A:PredCode	Prop Pups	B/A:Prop Pups	Group Size	B/A:Group Size	Rainfall 9Months	B/A:Rainfall 9Months	Rainfall 30Days	B/A:Rainfall 30Days	Max Temp	B/A:Max Temp	Max Temp:Rainfall 9Months	Max Temp:Rainfall 30Days	Group Size:Prop Pups	Forage:Pred Code	Forage:Max Temp	Forage:Rainfall 9Months	Forage:Rainfall3 0Days	Forage:Group Size	df	loglik	AICc	delta	weight	
e8	4.4	+													0.0	+									7	-	48941.	0.00	0.7	
	8														2												24463.	09		0.7
																											53			9
e1	4.6										0.3				0.0		-0.03								7	-	48945.	3.98	0.1	
	2										4				2												24465.	07		0.1
																											52			1
e1	4.5												4.0	0.0			-								7	-	48945.	4.15	0.1	
	3												8	2			0.17										24465.	24		0
																											61			0
e6	5.3	+									-	+													7	-	48957.	15.9	0.0	
	0										1.1																24471.	00	1	0
											7																49			0
e2	4.6														0.0										5	-	48957.	16.3	0.0	
	2														2												24473.	42	3	0
																											70			0
e1	4.6		+												0.0						+				7	-	48959.	18.1	0.0	
	8														2												24472.	24	5	0
																											60			0
e1	5.3										-														5	-	48970.	29.4	0.0	
	1										1.1																24480.	51	2	0
											1																25			0

e1 9	5.3 4	+			- 1.0 8			+	7	- 24480. 01	48974. 04	32.9 5	0.0 0
e4	5.0 9	+		- 0.2 4	+				7	- 24495. 75	49005. 52	64.4 3	0.0 0
e1	5.0 8	+							5	- 24498. 64	49007. 30	66.2 1	0.0 0
e7	5.1 0	+			- 0.8 0	+			7	- 24497. 17	49008. 38	67.2 9	0.0 0
e5	5.1 4	+		0.0 0	+				7	- 24497. 35	49008. 73	67.6 4	0.0 0
e3	5.0 2	+	+	+					7	- 24497. 87	49009. 76	68.6 7	0.0 0
e2	5.0 9	+	+	+					7	- 24498. 27	49010. 56	69.4 7	0.0 0
e1 5	5.1 4			- 0.3 1					5	- 24504. 42	49018. 85	77.7 6	0.0 0
e2 3	5.1 4				- 0.6 6				5	- 24505. 82	49021. 65	80.5 6	0.0 0
e1 6	5.1 4			- 0.0 5	0.0 0			- 0.0 2	7	- 24503. 96	49021. 94	80.8 5	0.0 0
e9	5.0 9		+						5	- 24506. 55	49023. 11	82.0 2	0.0 0
e1 4	5.1 3	+							5	- 24507. 10	49024. 22	83.1 3	0.0 0

e1	5.1			0.0				5	-	49024.	83.1	0.0
0	5			0						24507.	27	8
										13		0
e2	5.1	+			-			7	-	49025.	84.5	0.0
0	5				0.6					24505.	59	0
					9					78		0
e1	5.0	+	+					7	-	49026.	84.9	0.0
7	7									24505.	01	2
										99		0
e2	5.1	+		0.0				7	-	49027.	86.7	0.0
1	4			0						24506.	86	7
										92		0

f. Pup provisioning

Table 8. – Model selection table for the factors affecting per pup provisioning rate ranked by AIC value. Variables tested are the hour before or after a recruitment event, proportion of pups in the group, predator cue type (scent or object), previous 30 day total rainfall, previous 9 month total rainfall, daily maximum temperature. Models forming the top set in bold.

	Intercept	ZI Intercept	Pred Code B/A	Pred Code B/A	Prop Pups	PropPups: B/A	Group Size	Group Size: B/A	Rainfall 9Months	B/A:Rainfall 9Months	Rainfall 30Days	B/A:Rainfall 30Days	Max Temp	Max Temp: B/A	Max Temp:Rainfall 30Days	Group Size:PropPups	MaxTemp:Rainfall9Months	MaxTemp:B/A:Rainfall 9Months	df	logLik	AICc	delta	weight
f1	0.1	-			-		0.0									-			8	-	3630.3	0.00	0.57
5	6	21.0			0.79		1									0.1			8	1807.13	8		
f1	0.3	-			-														6	-	3631.1	0.81	0.38
4	2	20.7			2.86														6	1809.56	9		
f3	0.2	-	+		-	+													8	-	3634.9	4.58	0.06
9	21.1	6			2.78	5													8	1809.42	6		
f2	-	-	+	+	+														8	-	3648.9	18.5	0.00
4	0.1	21.3																	8	1816.40	2	4	
f1	-	-							-										6	-	3650.8	20.4	0.00
1	0.1	20.7						0.9	0										6	1819.40	6	8	
f1	-	-					0.0												6	-	3651.3	20.9	0.00
0	0.5	21.0					1												6	1819.63	2	4	
f9	-	-	+																6	-	3652.6	22.3	0.00
6	0.4	20.9																	6	1820.31	9	1	
3	6	3																					

f1	0.0	-					0.0	-0.03	8	-	3653.3	22.9	0.00				
2	1	21.3				0.1	0			1818.59	0	2					
		4				9											
f1	-	-	+						6	-	3653.4	23.0	0.00				
	0.3	21.1								1820.68	2	4					
	3	9															
f1	-	-					-		6	-	3653.4	23.1	0.00				
7	0.2	20.8					0.50			1820.71	9	1					
	9	8															
f1	-	-							6	-	3653.6	23.2	0.00				
6	0.2	20.8					0			1820.77	2	4					
	4	7															
f5	-	-	+			-	+		8	-	3653.6	23.3	0.00				
	0.2	21.3				0.5				1818.78	8	0					
	1	0				5											
f4	-	-	+			0.0	+		8	-	3654.8	24.4	0.00				
	0.6	20.8				2				1819.37	6	7					
	5	4															
f1	-	-					-		8	-	3655.8	25.4	0.00				
3	0.0	13.2					10.8	0.0		1819.86	4	6					
	6	1					0	1									
f7	-	-	+					0.0	+	8	-	3657.0	26.6	0.00			
	0.3	20.8						0		1820.45	2	4					
	8	9															
f6	-	-	+				-	+	8	-	3657.2	26.8	0.00				
	0.3	20.3					0.35			1820.55	2	4					
	2	4															
f8	-	-	+			-	+		0.0	+	0.01	+	12	-	3658.4	28.1	0.00
	0.0	20.9				1.0		0						1817.12	9	1	
	6	3				0											

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