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26 **Kinship Dynamics: Patterns and Consequences of Changes in Local Relatedness**

27

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47

48 **Abstract**

49 Mounting evidence suggests that patterns of local relatedness can change over time in
50 predictable ways, a process termed kinship dynamics. Kinship dynamics may occur at the level
51 of the population or social group, where the mean relatedness across all members of the
52 population or group changes over time, or at the level of the individual where an individual's
53 relatedness to its local group changes with age. Kinship dynamics are likely to have
54 fundamental consequences for the evolution of social behaviour and life history because they
55 alter the inclusive fitness payoffs to actions taken at different points in time. For instance,
56 growing evidence suggests that individual kinship dynamics have shaped the evolution of
57 menopause and age-specific patterns of helping and harming. To date, however, the
58 consequences of kinship dynamics for social evolution have not been widely explored. Here
59 we review the patterns of kinship dynamics that can occur in natural populations and highlight
60 how taking a kinship dynamics approach has yielded new insights into behaviour and life
61 history evolution. We discuss areas where analysing kinship dynamics could provide new
62 insight into social evolution and we outline some of the challenges in predicting and
63 quantifying kinship dynamics in natural populations.

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76 For over half a century kin selection has been a cornerstone of evolutionary biology, providing
77 a fundamental theoretical framework for understanding the evolution of social behaviour [1].
78 When developing the theory of kin selection, Hamilton [1] recognised that a key factor
79 influencing kin structure is the degree to which individuals disperse away from their natal
80 habitat or social group. In Hamilton's original formalisation of kin selection, however, the
81 behavioural/demographic mechanisms by which the relatedness coefficient r was generated
82 were left undefined [1]. The effects of population structure and demography (group size and
83 dispersal rates) on patterns of local relatedness (mean pairwise relatedness to nearby
84 individuals) were explored by Taylor [2]. Rather than specifying the level of relatedness,
85 Taylor [2] allowed relatedness to emerge from the model. Taylor demonstrated that although a
86 decrease in dispersal generated an increase in local relatedness in structured populations, the
87 benefits of helping kin were cancelled out by the costs of an increase in competition among kin
88 [2]. In this pivotal finding, Taylor highlighted the importance of considering how dispersal
89 generates patterns of relatedness in structured populations. Over the last 30 years, a significant
90 focus of theoretical work has been in identifying the factors that influence local relatedness [3].
91 As well as patterns of dispersal, mating patterns, overlapping generations and social-partner
92 choice can all influence local relatedness [4-10].

93 Although often considered a static property of a group, population, or species, local relatedness
94 can be dynamic, changing predictably with time - referred to as kinship dynamics [11, 12].
95 When kinship dynamics are predictable and repeatable, then they may have profound
96 implications for social evolution [11, 12]. Currently, however, despite many species living in
97 kin-structured populations [13], studies of social evolution have tended not to consider the rich
98 implications of kinship dynamics. Here we review the different patterns of kinship dynamics
99 that can occur in natural populations and the potential consequences of kinship dynamics for
100 behaviour and life history evolution. We outline current gaps in our understanding of the
101 patterns and consequences of kinship dynamics and highlight priorities for future research.

102

103 **1. Patterns of Kinship Dynamics**

104 Here we identify three levels at which kinship dynamics may occur in natural populations (Fig
105 1). First, average local relatedness may change over time at the level of the population
106 (population kinship dynamics; Fig 1A). Second, kinship dynamics may occur at the group level
107 (group kinship dynamics), where the average local relatedness of members of a social group

108 changes over time (Fig 1B). Finally, kinship dynamics may occur at the individual level
109 (individual kinship dynamics), where the relatedness of a focal individual to its local group
110 changes systematically over time, often with age [11, 12] (Fig 1C). These levels can act either
111 independently or concurrently. For example, group level kinship dynamics may occur
112 independent of population kinship dynamics - the local mean relatedness of a social group may
113 change over time while the average local relatedness of the population remains constant over
114 time. Likewise, individual kinship dynamics do not imply population or group kinship
115 dynamics and the overall mean local relatedness (of a group or population) may remain
116 constant over time, even though the average relatedness of an individual female or male to the
117 rest of its group may increase or decrease.

118

119 **1.1. Population kinship dynamics**

120 Population kinship dynamics can be driven by temporal shifts in population density, fecundity
121 (reproductive success), reproductive skew, dispersal and mortality. For example, some species
122 of voles, mice and grouse exhibit cyclical kinship dynamics, linked to changes in population
123 density [14, 17, 18] (Fig 1A). For example, in male red grouse (*Lagopus lagopus scoticus*)
124 males form territories to gain access to females. In the autumn, young of the year males
125 compete to gain a territory and recruitment of males to a population is dependent on them
126 successfully securing a territory. At low population density, males are less aggressive towards
127 kin than non-kin and can even help young related males to gain a territory by relinquishing
128 territory or by helping in territorial contests with unrelated males [19]. This process forms
129 clusters of territories held by related males [20], which in turn generates a positive feedback
130 that leads to the proliferation of kin clusters. A point is reached, however, where space is
131 limited due to the density of the population and the inclusive fitness benefits of helping kin no
132 longer outweigh the direct costs of increased competition. At this point, cooperation breaks
133 down and all individuals behave aggressively. This suppresses recruitment of new males as
134 territory holders and the population spirals into decline and kin clusters break up [14]. This
135 process continues until the population reaches a point where competition is low and the males
136 once again start to help recruit related males to local territories setting the population off on
137 another cycle (Fig 1A).

138

139 Changes in patterns of reproductive success and survival may also change patterns of local
140 relatedness over time [21]. In China, for example, demographic transitions have resulted from

141 a reduction in the number of children per family (due to the country's family planning program)
142 while life expectancy has increased. The combined effects are a decline in the number of kin
143 relationships over time but the kin relationships that do occur are longer lasting [22].
144 Ecological forces such as predation risk and disease may generate substantial variation in
145 fecundity between groups, which can have consequences for population relatedness [23-25].
146 Under conditions where the variance in fecundity is high, for example, a predator wiping out
147 an entire family (clutch) of offspring, rather than removing individuals from multiple clutches,
148 then this can lead to high proportions of close kin being recruited to the population in
149 comparison to a scenario where mortality occurs at the level of the individual [25]. Cyclical
150 changes in predation or disease risk could, therefore, in theory, drive cyclical kinship dynamics
151 at the level of the population. The potential for such processes to drive population kinship
152 dynamics, however, remain uninvestigated.

153

154 **1.2. Group kinship dynamics**

155 At the level of the social group, local relatedness may be dynamic and change over time. Such
156 group level kinship dynamics can be driven by a range of demographic, social and ecological
157 factors. For example, in mammalian social groups, smaller groups, with higher reproductive
158 skew tend to have higher within-group average relatedness in comparison to larger groups [26-
159 28]. Changes in group size, for example, as a result of changes in the ecological environment,
160 may thus drive changes in patterns of relatedness within groups. Exactly how relatedness
161 changes with a change in group size, however, will depend on the process of group formation.
162 In banded mongooses (*Mungos mungo*), for example, new groups are founded when single sex
163 groups disperse from their natal group and join with groups of dispersers from other packs to
164 found a new group [15]. This "budding dispersal" can lead to an increase in local relatedness
165 with group age [15] (Fig 1B). In recently founded groups, relatedness between the sexes is low.
166 However, both males and females are highly philopatric, remaining in their natal group to
167 breed, this drives an increase in local relatedness between males and females with the age of
168 the group (Fig 1B). Such group based kinship dynamics can occur across multiple generations,
169 with the longevity of the social group exceeding the longevity of individuals [15]. The process
170 of group formation may be tightly linked to the quality of the environment, population density
171 and mortality rate. For example, in white-winged choughs (*Corcorax melanorhamphos*) new
172 groups were only observed after a period of unusually high mortality as a result of a drought
173 [29]. The process of new group formation was associated with reduced intra-group relatedness

174 due to fusions of unrelated groups/individuals [29]. At high population density, dispersal
175 opportunities may be limited, meaning that individuals are more likely to remain with their
176 local group [30] and thus changes in density at the local or population level may drive kinship
177 dynamics. In some social systems, relatedness may actually decline with the age of the social
178 group. For example, in several ant species, within-colony relatedness decreases with colony
179 age [e.g. 31, 32]. This is driven by new queens being more likely to remain in their natal colony
180 after mating, rather than dispersing to found new colonies as local colony density increases
181 [32, 33]. Thus increasing the number of queens within the colony (increasing polygyny),
182 diluting relatedness between workers and leading to long-term decreases in within-colony
183 relatedness.

184

185 Group fission may also be a key process leading to group level changes in kin structure. For
186 example, when the size of a social group exceeds the optimal group size, groups often split.
187 During such fission events, individuals may segregate based on kinship resulting in daughter
188 groups that are more assorted by kinship than the original group (e.g. [34, 35]). Group level
189 changes in kin structure may also be driven by group takeovers, whereby the dispersing sex
190 (usually males in the case of mammals), forcibly move into a group [36-38]. Such takeover
191 events are often associated with the eviction of residents of the same sex and the infanticide of
192 unrelated juvenile resident offspring [36-38]. If unrelated coalitions of males take over a group,
193 then reproduction may be shared among the males [38], which will reduce the relatedness of
194 resulting offspring in comparison to a group with high male reproductive skew. Group fission,
195 fusion and takeover events clearly have the potential to drive group kinship dynamics. To date,
196 however, previous work has not explicitly quantified patterns of kinship dynamics under these
197 social processes.

198

199 **1.3. Individual kinship dynamics**

200 Due to demographic processes – particularly the degree of philopatry and the extent of local
201 mating - local relatedness may change across an individual's lifetime (individual kinship
202 dynamics (Fig 1C)). Individual kinship dynamics were first formalised in theoretical models
203 examining the evolution of menopause in humans and some species of toothed whales [11, 12]
204 (see Fig 2). These models demonstrate that local relatedness can change as a function of age
205 as some individuals disperse from their natal group, and others die and are replaced by relatives
206 [11, 12]. Johnstone and Cant [12] investigated the consequences of different patterns of

207 dispersal and mating for changes in female local relatedness across the lifespan, highlighting
208 how demographic processes can drive individual kinship dynamics (Fig 2). Under sex biased
209 dispersal and within-group mating, the relatedness of the dispersing sex to their group (after
210 dispersal) is predicted to increase with age [11, 12] (Fig 2Aii). When the dispersing sex takes
211 up residency with their new social group, they will initially have low local relatedness. Their
212 relatedness, however, will increase with age as they reproduce and subsequently their
213 philopatric offspring reproduce and produce philopatric grand offspring, which they are related
214 to. Thus the increase in local relatedness for the dispersing individual joining a new social
215 group is driven by an increase in relatedness to the philopatric sex (Fig 2 Aii). Even when there
216 is no sex biased dispersal, kinship dynamics can still occur [12] (Fig 2 Aiii). For example, in
217 some species of toothed whales, neither sex disperses and mating occurs outside of the social
218 group. Under these conditions, females are born into a group without their father and have
219 comparatively low relatedness to males in the group. As females age and reproduce, their sons
220 will remain in the local group and their relatedness to local males is predicted to increase over
221 time [12]. Work to date on patterns of individual kinship dynamics has tended to consider the
222 general pattern of kinship dynamics at the level of the population for individuals belonging to
223 a particular class (e.g. males or females). However, within a given class of individuals, there is
224 likely considerable variation in the kinship dynamics that individuals experience, for example,
225 due to individual differences in dispersal and fecundity.

226

227 Few empirical studies have quantified age-dependent kinship dynamics in natural populations.
228 In a comparative study across 19 human communities with diverse patterns of residence and
229 dispersal, Koster et al. [39] examined the prediction that immigrants to a community will
230 initially have low relatedness to the local group with few kinship ties, but that their local
231 relatedness will increase as they populate the local group with their descendants [11, 12]. The
232 general predicted pattern was observed, with patterns of local relatedness increasing with age
233 in both immigrant males and females where they were the more commonly dispersing sex.
234 Some communities, however, displayed very different patterns, which were likely due to
235 unstable settlement histories, fluid patterns of residency and community size [39]. In human
236 societies, analysis of kinship dynamics could be extended to include affinal kin (in-laws) who
237 may be treated more like biological kin than unrelated friends [40], because they share genetic
238 interests in future generations [41].

239

240 Support for individual kinship dynamics also comes from work on non-human animals. For
241 example, in work on wild populations of killer whales that show bisexual philopatry, we have
242 found a strong match with the theoretical prediction of increasing female relatedness with age
243 (Fig 1C, Fig 2Aiii) [16]. Analogous patterns have been found in several species of cooperative
244 breeders where relatedness of an individual to the local group changes as a function of age [42-
245 44]. For example, in African wild dogs (*Lycaon pictus*), dwarf mongooses (*Helogale parvula*)
246 and Lake Tanganyika cichlids (*Neolamprologus pulcher*) the relatedness of non-breeding
247 helpers to the dominant breeders decreases with helper age due to a combination of breeder
248 turnover, extra-pair paternity and helper immigration [42-44].

249

250

251 **2. The consequences of kinship dynamics for social evolution**

252

253 Individual kinship dynamics may directly impact patterns of helping and harming behaviour
254 across the lifespan due to a change in the immediate availability of kin with age, which will
255 drive changes in patterns of social behaviour. However, when individual kinship dynamics
256 show predictable changes, they have the potential to influence the evolution of optimal life
257 history and behaviour [11, 12]. For example, models of life history evolution in humans and
258 toothed whales predict that kinship dynamics shape the selective pressures on reproductive
259 lifespan and can help explain why females undergo menopause [11, 12]. Under patterns of
260 kinship dynamics where female relatedness increases with age (which occurs in resident killer
261 whales (Fig 1C) and is thought to be the case in ancestral humans [11, 12]) younger females
262 are predicted to be under strong selection for harming behaviour, whereas older females are
263 under stronger selection for helping behaviour [11, 12 see Fig 2]. Cant and Johnstone
264 formalised these asymmetries in selection for helping and harming behaviour as the
265 reproductive conflict hypothesis, which predicts that when old and young females in the same
266 local group compete for reproduction, younger females should outcompete older females
267 (because they are under stronger selection for harming behaviour). When taken together with
268 the benefits grandmothers can gain by helping their kin (the grandmother hypothesis [49]) the
269 reproductive conflict hypothesis provides a mechanism to explain why females undergo
270 menopause – they are under selection to switch from a harming strategy where they reproduce
271 to a helping strategy where they invest in helping their kin and no longer reproduce themselves
272 [49]. There is strong support in both humans and killer whales that there is intergenerational
273 conflict between old and young females [16, 50, 51] and that this can contribute to selection

274 for the evolution of menopause. For example, in work on resident killer whales using over 40
275 years of individual-based demographic and social data we showed that when mothers and
276 daughters co-breed, the offspring from the older generation had a significantly higher risk of
277 mortality than offspring from the younger generation female [16].

278

279 Evolutionary models of individual kinship dynamics to date, have tended to focus on life
280 history trade-offs at a given point in time [11, 12]. Selection, however, may act on temporal
281 trade-offs between current vs future fitness, which will be shaped by individual kinship
282 dynamics. Such trade-offs would not require an individual to project likely changes in kinship
283 dynamics itself - selection on social traits will be influenced by the expected future kin structure
284 and the associated fitness costs and benefits. Although there has been little explicit analysis of
285 how kinship dynamics (i.e. changing levels of relatedness over time) influence inter-temporal
286 trade-offs, models have shown that kin selection can modulate the balance between current
287 and future costs and benefits (even when relatedness remains constant) [52, 53]. For example,
288 Lehmann [52] demonstrated that when there is a tendency for future members of an
289 individual's community to be kin, then selection can act on organisms in a way that produces
290 future benefits to its community. Sozou [53] extended this concept further to examine how an
291 individual should value future benefits to itself (individual discounting) or its social community
292 (social discounting), finding that the social discounting rate was generally lower than the
293 individual (private) discounting rate. The extension of kinship dynamic models to consider
294 temporal trade-offs and social/individual discounting provides an exciting avenue for future
295 research.

296

297 To date, models examining the evolutionary consequences of individual kinship dynamics have
298 been restricted to studies investigating the evolution of menopause in humans and toothed
299 whales. There is no reason to expect, however, that the behaviour and life-history implications
300 of kinship dynamics are restricted to the evolution of this unusual life-history trait. Kin
301 selection models have been integrated with life-history theory in considering the evolution of
302 senescence, where an individual's longevity can influence the vital rates of local relatives [54,
303 55]. If individuals can provide benefits to kin in late life it may select for longevity [49, 56-
304 58]. In support of this prediction, recent work comparing the longevity of females across non-
305 human mammals found that females in species with grandparental care lived longer [59]. Thus
306 we hypothesise that in species where relatedness increases with individual age selection will

307 favour longevity if there are opportunities for late life helping. The costs of interacting with
308 kin, which can reduce the fitness of relatives, may also drive life history evolution [54]. For
309 example, theoretical work has reported that low juvenile dispersal reduces the strength of
310 selection on adult survival [55], favouring the evolution of shorter lifespans [60, 61]. Thus we
311 predict that in species where interacting with kin carries significant costs, individual kinship
312 dynamics, where relatedness increases with age could result in selection for shorter lifespans.
313 Future research is needed to understand how kinship dynamics interact with both the
314 opportunities for helping kin and the costs of interacting with kin to shape the evolution of
315 senescence. Theoretical work has also shown that competition among kin can shape age-
316 specific fecundity [55]. When dispersal is limited and competition among siblings is intense,
317 selection will favour individuals to reduce competition among kin during times of peak fertility
318 and spread reproduction throughout life [55]. Kinship dynamics thus have the potential to shape
319 reproductive decisions across the lifespan, well beyond the evolution of menopause and new
320 work is needed to examine how kinship dynamics influence reproductive decisions across the
321 lifespan.

322

323 At the level of the group - group kinship dynamics generate the possibility that patterns of
324 helping and harming within and between groups may change over time. For example, in the
325 case of the banded mongoose, an increase in within-group relatedness will select for increased
326 helping within groups which could manifest as increased helping in rearing pups and/or
327 dominant individuals being more tolerant of the breeding attempts of related subordinate
328 individuals in older vs younger groups [15]. Moreover, in social groups that have high levels
329 of within-group relatedness selection can favour indiscriminate helping whereby individuals
330 do not adjust the level of help they provide other individuals within the group in response to
331 their relatedness to them [45]. Group based kinship dynamics may have consequences for the
332 success of the group. For example, in matrilineal groups of red howler monkeys, the average
333 group relatedness predicts female reproductive success with females in kin groups having
334 significantly higher reproductive success [46]. In addition, theoretical work has demonstrated
335 that changes in within-group or population relatedness can change the nature of intergroup
336 violence and warfare [47]. For example, an increase in within-group relatedness may increase
337 selection for belligerence and bravery behaviours, which can result in individuals paying a
338 personal cost of death so that relatives in the group can gain benefits such as new mating
339 opportunities or additional resources [47]. Predictable changes in patterns of local relatedness
340 at a group level may shape how social relationships form in groups. For example, one

341 possibility is that founding animals may invest more in forming stronger social relationships in
342 groups where kinship increases over time. Future empirical and theoretical work is needed to
343 examine the ontogeny of social relationships in social groups that are undergoing different
344 patterns of group kinship dynamics.

345

346 Because kin selection is conditional on the kin structure in the social environment, kinship
347 dynamics may result in cyclical shifts in selection which could reduce the long term efficiency
348 of kin selection [48]. Under population and group kinship dynamics, which can occur across
349 many generations, different social traits may be selected for under different levels of local
350 relatedness. Such condition-dependent selection may dilute the strength of selection when
351 social conditions change across generations or differ between social groups [48]. In periods
352 when social traits are not under strong selection, genetic drift may be enhanced, which can lead
353 to accelerated evolution – referred to as the Red King process [48]. The efficiency of kin
354 selection thus may be weaker under greater conditionality (i.e. when periods of high relatedness
355 occur infrequently). Future work is needed to directly explore the consequences of population
356 and group kinship dynamics for the efficiency of kin selection.

357

358 **3. Predicting and quantifying individual kinship dynamics**

359

360 Current models predicting patterns of kinship dynamics have tended to focus on the
361 consequences of variation in dispersal and mating [11, 12]. It is likely however that other
362 factors also play a role in driving kinship dynamics in animal societies, including group size,
363 mortality patterns and variation in fecundity. How well model predictions match empirical
364 patterns of kinship dynamics will depend on how well they capture the key processes driving
365 relatedness patterns [26]. Some insight into how population traits other than dispersal and
366 mating patterns may influence individual kinship dynamics comes from a study by Rodrigues
367 [62] who examined how variation in age-dependent changes in patterns of fecundity drive age-
368 dependent kinship dynamics which in turn is expected to drive age-dependent patterns of
369 helping behaviour. Rodrigues found that in populations where fecundity increases with age,
370 the average local relatedness of an individual to their local group is predicted to increase with
371 age, which will select for an increase in helping with the actor's age. In predicting patterns of
372 kinship dynamics, it is important to accurately evaluate demographic features of the population
373 that can drive kinship dynamics (e.g. dispersal patterns). In some instances, the predictability

374 of kinship dynamics may be limited due to stochasticity in demographic variables (including,
375 for example, mortality, reproductive success and dispersal).

376

377 New work is needed to fully examine how demographic and life history traits impact on
378 patterns of kinship dynamics. Kinship dynamics are likely to show considerable differences
379 between the sexes. For example, work in humans illustrates that kinship dynamics can show
380 surprisingly diverse patterns across communities and the sexes [39] with local relatedness both
381 increasing and decreasing as a function of age. In the vast majority of natural populations, there
382 is a bias towards one sex dispersing. It is well documented that sex differences in dispersal
383 mean that kin selection can affect males and females very differently [63]. Currently, however,
384 how the sexes differ in patterns of kinship dynamics and the resulting implications for sex
385 differences in life history evolution remains unexplored. Moreover, within a sex it is well
386 documented that both dispersal patterns [64] and reproductive success can vary among
387 individuals, which will generate inter-individual variation in kinship dynamics. The
388 consequences of this inter-individual variation in patterns of kinship dynamics for social
389 evolution has not been explored.

390

391 To quantify patterns of kinship dynamics, we need to decide how to quantify local relatedness.
392 In species where individuals form stable social groups, we can track patterns of kinship by
393 examining patterns of relatedness between individuals within a local group over time.
394 However, in many animal societies, social groups are dynamic and individuals interact and
395 cooperate with animals from different social units. Here we need to capture social interactions
396 within and between groups. One approach is to use social network theory and community
397 detection algorithms to define local kinship networks [65]. It would then be possible to quantify
398 local kin structure using weighted measures of association strength, using association indices
399 [66] to weight relatedness between individuals by the strength (weight) of their association.

400

401 **4. Conclusions**

402

403 Kinship dynamics mean that the strength and direction of kin selection can change
404 systematically over time [11, 12, 16, 62]. To date however, very few studies have incorporated
405 kinship dynamics into models of social evolution. Current theory, predicting the evolutionary
406 consequences of kinship dynamics has tended to focus on species that undergo menopause.

407 However, the evolutionary consequences of kinship dynamics are likely to extend well beyond
408 this unusual life history trait and new work is needed to develop a general understanding of the
409 evolutionary consequences of kinship dynamics at the level of the population, group and
410 individual.

411

412 A particularly exciting avenue for future research is the comparison of kinship dynamics
413 between the sexes. Life history differences between the sexes within a species are widespread
414 and significant attention has been given to examining the mechanisms driving sex differences
415 in life history evolution [67]. It is possible that in many species, the sexes experience very
416 different patterns of kinship dynamics that could have been a significant force driving sex
417 differences in life history evolution. Because kinship dynamics are driven by demographic
418 processes, kinship dynamics are likely to show profound differences between species. For
419 example, individual kinship dynamics are dependent on patterns of philopatry, the general
420 pattern of which differs between birds and mammals (e.g. in birds females normally disperse
421 more than males whereas in contrast in mammals males typically disperse more than females
422 [68]) leading to the prediction that general patterns of kinship dynamics may differ between
423 taxa. Moreover, because group size, predation and fecundity likely play a key role in driving
424 patterns of kinship dynamics, it is likely that patterns of kinship dynamics differ between
425 populations of the same species living under different ecological conditions. Future work
426 comparing patterns of kinship dynamics between species, populations and the sexes is eagerly
427 anticipated.

428

429 Patterns of kinship dynamics may help explain variation in social behaviour across the lifespan
430 and contribute to patterns of social ageing. In humans and non-human primates there may be
431 fundamental shifts in social interactions as individuals age [69]. This can include the propensity
432 to engage in social interactions, the capability to influence others and the positive vs negative
433 valence of social interactions [70]. How patterns of individual kinship dynamics influence the
434 cost-benefit trade-off of social interactions across the lifespan and thus patterns of social ageing
435 remains unexplored.

436

437 Future research should examine how active partner preferences shape kinship dynamics and
438 how individuals respond to demographic events in their social network and the consequences
439 of these events for kinship dynamics. For example, long term observations on female baboons

440 (*Papio cynocephalus*) has shown that following a mother's death, maternal sisters strengthen
441 their social bond whereas the bonds with maternal aunts are weakened [71]. Feedbacks may
442 exist between changes in behaviour and changes in relatedness that generate further changes in
443 relatedness and behaviour. For example, excluding individuals from groups to minimise
444 competition could generate increases in local relatedness which further selects for increased
445 investment exclusion (since this is an altruistic act that benefits everyone in the group, it is
446 favoured by higher r). In principle, this kind of positive feedback could lead to a runaway
447 outcome that results in a very high level of local relatedness over time. Such feedbacks
448 however, have not been formalised in models of group formation and social evolution,
449 providing an exciting opportunity for future research.

450

451 Here we have focused on changes in local relatedness over time, however, the other terms in
452 Hamilton's rule – the costs (c) and benefits (b) may also change over time [72] and interact
453 with individual kinship dynamics. For example, reproductive value (the expected contribution
454 of an individual to the future population) can significantly impact kin directed behaviours [73].
455 The costs of a social act depend in part on the reproductive value of the actor and the benefits
456 on the reproductive value of the recipient, both of which can change with age [74]. In many
457 species, the ability of individuals to help and provide benefits to kin may also be age-dependent
458 [75]. For example, as individuals age, they develop skills, knowledge and experience that
459 increase the benefits they can pass on to kin [76-79]. For example, in African elephants
460 (*Loxodonta africana*) older females are better able to assess social and predatory threats, which
461 can increase the survival of their younger kin [78, 79]. Similar results have been reported in
462 resident killer whales where old post-reproductive females lead their group around foraging
463 grounds, especially in times of low food abundance [77]. Kinship dynamic models provide a
464 conceptual framework to be able to examine how changes in patterns of local relatedness with
465 age interact with changes in the costs and benefits of social acts.

466

467 Given the ubiquity of kin-structured social groups in populations [13], kinship dynamics are
468 likely to have widespread consequences for the evolution of social behaviour and life history
469 in both males and females. Researchers working on kin structured social species often have the
470 data needed to quantify kinship dynamics. We encourage researchers to consider patterns of
471 kinship dynamics in their study systems and the potential consequences that they may have for
472 social evolution.

473

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480
481

482 **References**

- 483 1. Hamilton W.D. 1964 The genetical evolution of social behaviour. I and II. *J Theor*
484 *Biol* **7**(1), 1-52 [10.1016/0022-5193\(64\)90039-6](https://doi.org/10.1016/0022-5193(64)90039-6).
- 485 2. Taylor P. 1992 Altruism in viscous populations—an inclusive fitness model.
486 *Evolutionary Ecology* **6**(4), 352-356 <https://doi.org/10.1007/BF02270971>.
- 487 3. Cooper G.A., Levin S.R., Wild G., West S.A. 2018 Modeling relatedness and
488 demography in social evolution. *Evol Lett* **2**(4), 260-271 <https://doi.org/10.1002/evl3.69>.
- 489 4. Boomsma J.J. 2007 Kin selection versus sexual selection: why the ends do not meet.
490 *Curr Biol* **17**(16), R673-R683 <https://doi.org/10.1016/j.cub.2007.06.033>.
- 491 5. Boomsma J.J. 2009 Lifetime monogamy and the evolution of eusociality. *Philos*
492 *Trans R Soc Lond B Biol Sci* **364**(1533), 3191-3207 [10.1098/rstb.2009.0101](https://doi.org/10.1098/rstb.2009.0101).
- 493 6. Lukas D., Clutton-Brock T. 2012 Cooperative breeding and monogamy in
494 mammalian societies. *Proc R Soc Biol Sci Ser B* **279**(1736), 2151–2156
495 [10.1098/rspb.2011.2468](https://doi.org/10.1098/rspb.2011.2468).
- 496 7. Eliassen S., Jørgensen C. 2014 Extra-pair mating and evolution of cooperative
497 neighbourhoods. *PLOS ONE* **9**(7), e99878 [10.1371/journal.pone.0099878](https://doi.org/10.1371/journal.pone.0099878).
- 498 8. Taylor P.D., Irwin A.J. 2000 Overlapping generations can promote altruistic behavior.
499 *Evolution* **54**(4), 1135-1141
- 500 9. Sharp S.P., McGowan A., Wood M.J., Hatchwell B.J. 2005 Learned kin recognition
501 cues in a social bird. *Nature* **434**(7037), 1127-1130 [10.1038/nature03522](https://doi.org/10.1038/nature03522).
- 502 10. Vastenhouw N., Brunschwig K., Okihara K., Müller F., Tijsterman M., Plasterk R.
503 2006 Social evolution: kin preference in a social microbe. *Nature* **442**, 882
504 <https://doi.org/10.1038/442881a>.

- 505 11. Cant M.A., Johnstone R.A. 2008 Reproductive conflict and the separation of
506 reproductive generations in humans. *Proc Natl Acad Sci USA Biol Sci* **105**(14), 5332-5336
507 10.1073/pnas.0711911105.
- 508 12. Johnstone R.A., Cant M.A. 2010 The evolution of menopause in cetaceans and
509 humans: the role of demography. *Proc R Soc Biol Sci Ser B* **277**(1701), 3765-3771
510 10.1098/rspb.2010.0988.
- 511 13. Hatchwell B.J. 2010 Cryptic kin selection: kin structure in vertebrate populations and
512 opportunities for kin-directed cooperation. *Ethology* **116**(3), 203-216
513 <https://doi.org/10.1111/j.1439-0310.2009.01732.x>.
- 514 14. Piertney S.B., Lambin X., Maccoll A.D., Lock K., Bacon P.J., Dallas J.F., Leckie F.,
515 Mougeot F., Racey P.A., Redpath S. 2008 Temporal changes in kin structure through a
516 population cycle in a territorial bird, the red grouse *Lagopus lagopus scoticus*. *Mol Ecol*
517 **17**(10), 2544-2551 <https://doi.org/10.1111/j.1365-294X.2008.03778.x>.
- 518 15. Nichols H.J., Jordan N.R., Jamie G.A., Cant M.A., Hoffman J.I. 2012 Fine-scale
519 spatiotemporal patterns of genetic variation reflect budding dispersal coupled with strong
520 natal philopatry in a cooperatively breeding mammal. *Mol Ecol* **21**(21), 5348-5362
521 10.1111/mec.12015.
- 522 16. Croft D.P., Johnstone R.A., Ellis S., Natrass S., Franks D.W., Brent L.J., Mazzi S.,
523 Balcomb K.C., Ford J.K., Cant M.A. 2017 Reproductive conflict and the evolution of
524 menopause in killer whales. *Curr Biol* **27**(2), 298-304 10.1016/j.cub.2016.12.015.
- 525 17. Borkowska A., Ratkiewicz M. 2004 Seasonal changes of population genetic structure
526 and relatedness in the bank vole *Clethrionomys glareolus*: An analysis of age cohorts. *Ann*
527 *Zool Fenn*, 661-670
- 528 18. Moss R., Watson A. 1991 Population cycles and kin selection in red grouse *Lagopus*
529 *lagopus scoticus*. *Ibis* **133**, 113-120 <https://doi.org/10.1111/j.1474-919X.1991.tb07674.x>.
- 530 19. MacColl A.D., Piertney S.B., Moss R., Lambin X. 2000 Spatial arrangement of kin
531 affects recruitment success in young male red grouse. *Oikos* **90**(2), 261-270
532 <https://doi.org/10.1034/j.1600-0706.2000.900206.x>.
- 533 20. Piertney S.B., MacColl A.D.C., Lambin X., Moss R., Dallas J.F. 1999 Spatial
534 distribution of genetic relatedness in a moorland population of red grouse (*Lagopus lagopus*
535 *scoticus*). *Biol J Linn Soc* **68**(1-2), 317-331
- 536 21. Caswell H. 2019 The formal demography of kinship: A matrix formulation. *Demogr*
537 *Res* **41**(24), 679-712 10.4054/DemRes.2019.41.24.

- 538 22. Jiang L. 1995 Changing kinship structure and its implications for old-age support in
539 urban and rural China. *Popul Stud* **49**(1), 127-145
540 <https://doi.org/10.1080/0032472031000148286>
- 541 23. Lehmann L., Balloux F.o. 2007 Natural selection on fecundity variance in subdivided
542 populations: Kin selection meets bet hedging. *Genetics* **176**(1), 361-377
543 10.1534/genetics.106.066910.
- 544 24. Lehmann L., Rousset F. 2010 How life history and demography promote or inhibit the
545 evolution of helping behaviours. *Philosophical Transactions of the Royal Society B:*
546 *Biological Sciences* **365**(1553), 2599-2617 doi:10.1098/rstb.2010.0138.
- 547 25. Beckerman A.P., Sharp S.P., Hatchwell B.J. 2011 Predation and kin-structured
548 populations: an empirical perspective on the evolution of cooperation. *Behav Ecol* **22**(6),
549 1294-1303 10.1093/beheco/arr131.
- 550 26. Lukas D., Reynolds V., Boesch C., Vigilant L. 2005 To what extent does living in a
551 group mean living with kin? *Mol Ecol* **14**(7), 2181-2196 [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-294X.2005.02560.x)
552 [294X.2005.02560.x](https://doi.org/10.1111/j.1365-294X.2005.02560.x).
- 553 27. Alvard M.S. 2003 Kinship, lineage, and an evolutionary perspective on cooperative
554 hunting groups in Indonesia. *Human Nature* **14**(2), 129-163 10.1007/s12110-003-1001-5.
- 555 28. Spong G., Stone J., Creel S., Björklund M. 2002 Genetic structure of lions (*Panthera*
556 *leo* L.) in the Selous Game Reserve: implications for the evolution of sociality. *J Evol Biol*
557 **15**(6), 945-953 <https://doi.org/10.1046/j.1420-9101.2002.00473.x>.
- 558 29. Heinsohn R., Dunn P., Legge S., Double M. 2000 Coalitions of relatives and
559 reproductive skew in cooperatively breeding white-winged choughs. *Proceedings of the*
560 *Royal Society of London Series B: Biological Sciences* **267**(1440), 243-249
561 <https://doi.org/10.1098/rspb.2000.0993>.
- 562 30. Hatchwell B.J. 2009 The evolution of cooperative breeding in birds: kinship, dispersal
563 and life history. *Philosophical Transactions of the Royal Society B: Biological Sciences*
564 **364**(1533), 3217-3227 doi:10.1098/rstb.2009.0109.
- 565 31. Seppä P., Sundström L., Puntitila P. 1995 Facultative polygyny and habitat succession
566 in boreal ants. *Biol J Linn Soc* **56**(4), 533-551 [https://doi.org/10.1016/0024-4066\(95\)90003-9](https://doi.org/10.1016/0024-4066(95)90003-9).
- 567 32. Ingram K.K. 2002 Plasticity in queen number and social structure in the invasive
568 argentine ant (*Linepithema humile*). *Evolution* **56**(10), 2008-2016
569 <https://doi.org/10.1111/j.0014-3820.2002.tb00127.x>.

- 570 33. Pedersen J.S., Boomsma J.J. 1999 Effect of habitat saturation on the number and
571 turnover of queens in the polygynous ant, *Myrmica sulcinodis*. *J Evol Biol* **12**(5), 903-917
572 <https://doi.org/10.1046/j.1420-9101.1999.00109.x>.
- 573 34. Widdig A., Nürnberg P., Bercovitch F.B., Trefilov A., Berard J.B., Kessler M.J.,
574 Schmidtke J., Streich W.J., Krawczak M. 2006 Consequences of group fission for the
575 patterns of relatedness among rhesus macaques. *Mol Ecol* **15**(12), 3825-3832 10.1111/j.1365-
576 294X.2006.03039.x.
- 577 35. Chepko-Sade B.D., Olivier T.J. 1979 Coefficient of genetic relationship and the
578 probability of intragenealogical fission in *Macaca mulatta*. *Behav Ecol Sociobiol* **5**(3), 263-
579 278 10.1007/BF00293675.
- 580 36. Morelli T.L., King S.J., Pochron S.T., Wright P.C. 2009 The rules of disengagement:
581 takeovers, infanticide, and dispersal in a rainforest lemur, *Propithecus edwardsi*. *Behaviour*
582 **146**(4-5), 499-523
- 583 37. Packer C., Pusey A.E. 1983 Adaptations of Female Lions to Infanticide by Incoming
584 Males. *Am Nat* **121**(5), 716-728 10.1086/284097.
- 585 38. Packer C., Pusey A.E. 1982 Cooperation and competition within coalitions of male
586 lions: kin selection or game theory? *Nature* **296**(5859), 740-742 10.1038/296740a0.
- 587 39. Koster J., Lukas D., Nolin D., Power E., Alvergne A., Mace R., Ross C.T., Kramer
588 K., Greaves R., Caudell M., et al. 2019 Kinship ties across the lifespan in human
589 communities. *Philosophical Transactions of the Royal Society B: Biological Sciences*
590 **374**(1780), 20180069 doi:10.1098/rstb.2018.0069.
- 591 40. Burton-Chellew M.N., Dunbar R.I.M. 2011 Are affines treated as biological kin? A
592 test of hughes's hypothesis. *Curr Anthropol* **52**(5), 741-746 10.1086/661288.
- 593 41. Hughes A.L. 1988 *Evolution and human kinship*. New York, Oxford University Press.
- 594 42. Creel S., Creel N.M. 2019 Patterns of relatedness and the fitness consequences of
595 dispersal, philopatry, and reproductive suppression. In *The African Wild Dog*, pp. 223-244,
596 Princeton University Press.
- 597 43. Creel S.R., Waser P.M. 1997 Variation in reproductive suppression among dwarf
598 mongooses: interplay between mechanisms and evolution. In *Cooperative breeding in*
599 *mammals* eds. Soloman N., French J., pp. 150-170. Cambridge, UK, Cambridge University
600 Press.
- 601 44. Dierkes P., Heg D., Taborsky M., Skubic E., Achmann R. 2005 Genetic relatedness in
602 groups is sex-specific and declines with age of helpers in a cooperatively breeding cichlid.
603 *Ecol Lett* **8**(9), 968-975 10.1111/j.1461-0248.2005.00801.x.

- 604 45. Duncan C., Gaynor D., Clutton-Brock T., Dyble M. 2019 The evolution of
605 indiscriminate altruism in a cooperatively breeding mammal. *Am Nat* **193**(6), 841-851
606 10.1086/703113.
- 607 46. Pope T.R. 2000 Reproductive success increases with degree of kinship in cooperative
608 coalitions of female red howler monkeys (*Alouatta seniculus*). *Behav Ecol Sociobiol* **48**(4),
609 253-267 10.1007/s002650000236.
- 610 47. Lehmann L., Feldman M.W. 2008 War and the evolution of belligerence and bravery.
611 *Proc R Soc Biol Sci Ser B* **275**(1653), 2877-2885 10.1098/rspb.2008.0842.
- 612 48. de Oliveira J.L., Morales A.C., Stewart B., Gruenheit N., Engelmoer J., Brown S.B.,
613 de Brito R.A., Hurst L.D., Urrutia A.O., Thompson C.R.L., et al. 2019 Conditional
614 expression explains molecular evolution of social genes in a microbe. *Nat Commun* **10**(1),
615 3284 10.1038/s41467-019-11237-2.
- 616 49. Hawkes K., O'Connell J.F., Jones N.B., Alvarez H., Charnov E.L. 1998
617 Grandmothering, menopause, and the evolution of human life histories. *Proc Natl Acad Sci*
618 *USA Biol Sci* **95**(3), 1336-1339 10.1073/pnas.95.3.1336.
- 619 50. Lahdenperä M., Gillespie D.O.S., Lummaa V., Russell A.F. 2012 Severe
620 intergenerational reproductive conflict and the evolution of menopause. *Ecol Lett* **15**(11),
621 1283-1290 10.1111/j.1461-0248.2012.01851.x.
- 622 51. Mace R., Alvergne A. 2012 Female reproductive competition within families in rural
623 Gambia. *Proc R Soc Biol Sci Ser B* **279**(1736), 2219-2227 10.1098/rspb.2011.2424.
- 624 52. Lehmann L. 2007 The evolution of trans-generational altruism: kin selection meets
625 niche construction. *J Evol Biol* **20**(1), 181-189 [https://doi.org/10.1111/j.1420-](https://doi.org/10.1111/j.1420-9101.2006.01202.x)
626 [9101.2006.01202.x](https://doi.org/10.1111/j.1420-9101.2006.01202.x).
- 627 53. Sozou P.D. 2009 Individual and social discounting in a viscous population.
628 *Proceedings of the Royal Society B: Biological Sciences* **276**(1669), 2955-2962
629 <https://doi.org/10.1098/rspb.2009.0401>.
- 630 54. Bourke A.F. 2007 Kin selection and the evolutionary theory of aging. *Annu Rev Ecol*
631 *Evol Syst* **38**, 103-128 <https://doi.org/10.1146/annurev.ecolsys.38.091206.095528>.
- 632 55. Ronce O., Promislow D. 2010 Kin competition, natal dispersal and the moulding of
633 senescence by natural selection. *Proc R Soc Biol Sci Ser B* **277**(1700), 3659-3667
634 10.1098/rspb.2010.1095.
- 635 56. Lee R.D. 2003 Rethinking the evolutionary theory of aging: transfers, not births,
636 shape senescence in social species. *Proc Natl Acad Sci USA Biol Sci* **100**(16), 9637-9642
637 <https://doi.org/10.1073/pnas.1530303100>.

- 638 57. Pavard S., Koons D.N., Heyer E. 2007 The influence of maternal care in shaping
639 human survival and fertility. *Evolution* **61**(12), 2801-2810 10.1111/j.1558-
640 5646.2007.00236.x.
- 641 58. Hawkes K., Smith K.R. 2010 Do women stop early? Similarities in fertility decline in
642 humans and chimpanzees. *Ann N Y Acad Sci* **1204**(1), 43-53 10.1111/j.1749-
643 6632.2010.05527.x.
- 644 59. Péron G., Bonenfant C., Lemaitre J.-F., Ronget V., Tidiere M., Gaillard J.-M. 2019
645 Does grandparental care select for a longer lifespan in non-human mammals? *Biol J Linn Soc*
646 **128**(2), 360-372 <https://doi.org/10.1093/biolinnean/blz078>.
- 647 60. Pen I. 2000 Reproductive effort in viscous populations. *Evolution* **54**(1), 293-297
648 10.1111/j.0014-3820.2000.tb00030.x.
- 649 61. Travis J.M. 2004 The evolution of programmed death in a spatially structured
650 population. *J Gerontol A Biol Sci Med Sci* **59**(4), B301-B305 10.1093/gerona/59.4.b301.
- 651 62. Rodrigues A.M. 2018 Demography, life history and the evolution of age-dependent
652 social behaviour. *J Evol Biol* **31**(9), 1340-1353 10.1111/jeb.13308.
- 653 63. Johnstone R.A., Cant M.A. 2008 Sex differences in dispersal and the evolution of
654 helping and harming. *American Naturalist* **172**(3), 318-330 10.1086/589899.
- 655 64. Gibbs M., Saastamoinen M., Coulon A., Stevens V.M. 2010 Organisms on the move:
656 ecology and evolution of dispersal. *The Royal Society*,
657 <https://doi.org/10.1098/rsbl.2009.0820>.
- 658 65. Croft D.P., James R., Krause J. 2008 *Exploring animal social networks*. Princeton,
659 NJ, Princeton University Press.
- 660 66. Whitehead H. 2008 *Analyzing animal societies: quantitative methods for vertebrate*
661 *social analysis*. Chicago, University of Chicago Press.
- 662 67. Maklakov A.A., Lummaa V. 2013 Evolution of sex differences in lifespan and aging:
663 causes and constraints. *BioEssays* **35**(8), 717-724 10.1002/bies.201300021.
- 664 68. Greenwood P.J. 1980 Mating systems, philopatry and dispersal in birds and
665 mammals. *Anim Behav* **28**, 1140-1162 [https://doi.org/10.1016/S0003-3472\(80\)80103-5](https://doi.org/10.1016/S0003-3472(80)80103-5).
- 666 69. Rosati A.G., Hagberg L., Enigk D.K., Otali E., Emery Thompson M., Muller M.N.,
667 Wrangham R.W., Machanda Z.P. 2020 Social selectivity in aging wild chimpanzees. *Science*
668 **370**(6515), 473-476 10.1126/science.aaz9129.
- 669 70. Machanda Z.P., Rosati A.G. 2020 Shifting sociality during primate ageing. *Philos*
670 *Trans R Soc Lond B Biol Sci* **375**(1811), 20190620 doi:10.1098/rstb.2019.0620.

- 671 71. Silk J.B., Altmann J., Alberts S.C. 2006 Social relationships among adult female
672 baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behav Ecol*
673 *Sociobiol* **61**(2), 183-195 [10.1007/s00265-006-0249-2](https://doi.org/10.1007/s00265-006-0249-2).
- 674 72. Houston A.I., McNamara J.M. 1999 *Models of adaptive behaviour: an approach*
675 *based on state*, Cambridge University Press.
- 676 73. Hasegawa M., Kutsukake N. 2019 Kin selection and reproductive value in social
677 mammals. *J Ethol* **37**(2), 139-150 <https://doi.org/10.1007/s10164-019-00586-6>.
- 678 74. Milinski M. 1978 Kin selection and reproductive value. *Zeitschrift für*
679 *Tierpsychologie* **47**(3), 328-329 <https://doi.org/10.1111/j.1439-0310.1978.tb01841.x>.
- 680 75. Li L., Peng H., Kurths J., Yang Y., Schellnhuber H.J. 2014 Chaos–order transition in
681 foraging behavior of ants. *Proc Natl Acad Sci USA Biol Sci* **111**(23), 8392-8397
682 [10.1073/pnas.1407083111](https://doi.org/10.1073/pnas.1407083111).
- 683 76. Smith J.E., Estrada J.R., Richards H.R., Dawes S.E., Mitsos K., Holekamp K.E. 2015
684 Collective movements, leadership and consensus costs at reunions in spotted hyaenas. *Anim*
685 *Behav* **105**, 187-200 <https://doi.org/10.1016/j.anbehav.2015.04.023>.
- 686 77. Brent L.J.N., Franks D.W., Foster E.A., Balcomb K.C., Cant M.A., Croft D.P. 2015
687 Ecological knowledge, leadership, and the evolution of menopause in killer whales. *Curr Biol*
688 **25**(6), 746-750 [10.1016/j.cub.2015.01.037](https://doi.org/10.1016/j.cub.2015.01.037).
- 689 78. McComb K., Moss C., Durant S.M., Baker L., Sayialel S. 2001 Matriarchs as
690 repositories of social knowledge in African elephants. *Science* **292**(5516), 491-494
691 [10.1126/science.1057895](https://doi.org/10.1126/science.1057895).
- 692 79. McComb K., Shannon G., Durant S., Sayiale K., Slotow R., Poole J., Moss C. 2011
693 Leadership in elephants: the adaptive value of age. *Proc R Soc Biol Sci Ser B* **278**(1722),
694 3270 - 3276 [10.1098/rspb.2011.0168](https://doi.org/10.1098/rspb.2011.0168).

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700 **Figure 1.** Examples of different patterns of kinship dynamics. (A) Population kinship dynamics
701 in red grouse (*Lagopus lagopus scoticus*) using data from an 8-year cycle in a natural
702 population [figure redrawn from 14]. Here kinship dynamics show a cyclical pattern with local
703 relatedness increasing during population growth as established males help related males to
704 establish a neighbouring breeding territory. As population density increases the costs of
705 competition with neighbouring kin outweighs the benefits leading to increasing aggression and
706 the break-up of kin clusters. (B) Group kinship dynamics of male – female relatedness in social
707 groups of banded mongoose (*Mungos mungo*). New social groups form by the fission of
708 unrelated male and female groups. As social groups age, male-female relatedness increases due
709 to philopatric males and females inheriting the breeding positions [figure redrawn from 15].
710 (C) Individual kinship dynamics in Northern and Southern resident killer whales (*Orcinus*
711 *orca*) showing patterns of maternal relatedness with female age for a total of 200 whales over
712 846 whale-years [figure redrawn from 16]. Figure shows the relationship between female age
713 and mean relatedness to other females (red line), males (blue line) and average relatedness
714 across both sexes (black line). Standard error of mean relatedness across both sexes is shown
715 as dotted lines. As females age, their local relatedness to the group increases due to an increase
716 in local relatedness to males. Animal images from PhyloPic: red grouse image (uncredited)
717 published under Public Domain Dedication 1.0 license
718 (<https://creativecommons.org/publicdomain/zero/1.0/>); banded mongoose image by Birgit
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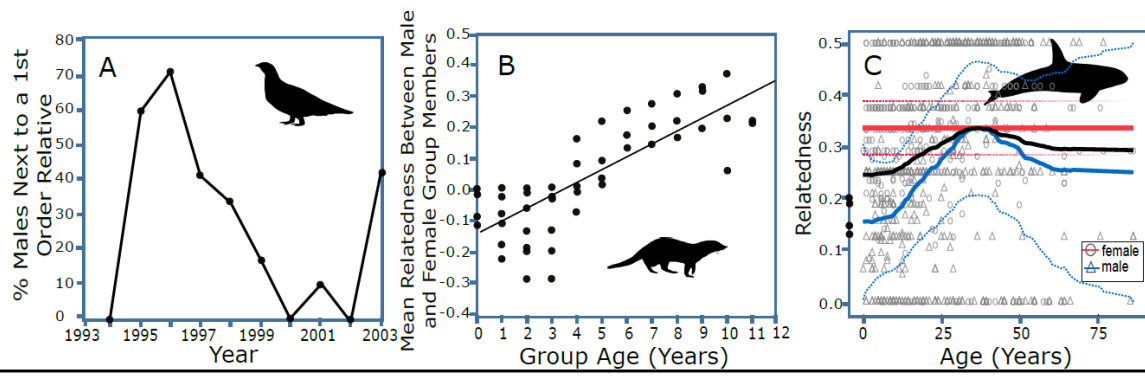
725 **Figure 2.** Age-dependent kinship dynamics and their consequences for selection on social traits
726 under different demographic patterns (modified from [12]). A) Predicted age-dependent
727 kinship dynamics, showing age-specific relatedness to a breeding female of other local males
728 (dotted lines) and females (solid lines) and the average relatedness across both sexes (dashed
729 line). Age is scaled in mean generation lengths. Three different demographic patterns are
730 plotted: (i) local mating within the group with high male dispersal and low female dispersal;
731 (ii) local mating within the group with low male dispersal and high female dispersal; (iii) non-
732 local mating (i.e. mating occurs outside the group) with low dispersal by both sexes. B). The

733 consequences of age-dependent kinship dynamics for selection for helping (boosting the
734 fecundity of other local breeders) and harming (reducing the fecundity of other local breeders)
735 across the lifespan under different demographic patterns (i-iii as in A). A focal female can
736 perform social acts that result in an immediate gain of b offspring for other breeders at an
737 immediate cost c to herself. Selection for helping and harming are indicated by shading on the
738 graph with blue areas indicating selection for helping and red areas indicate selection for
739 harming. For further details, see Johnstone & Cant [12].

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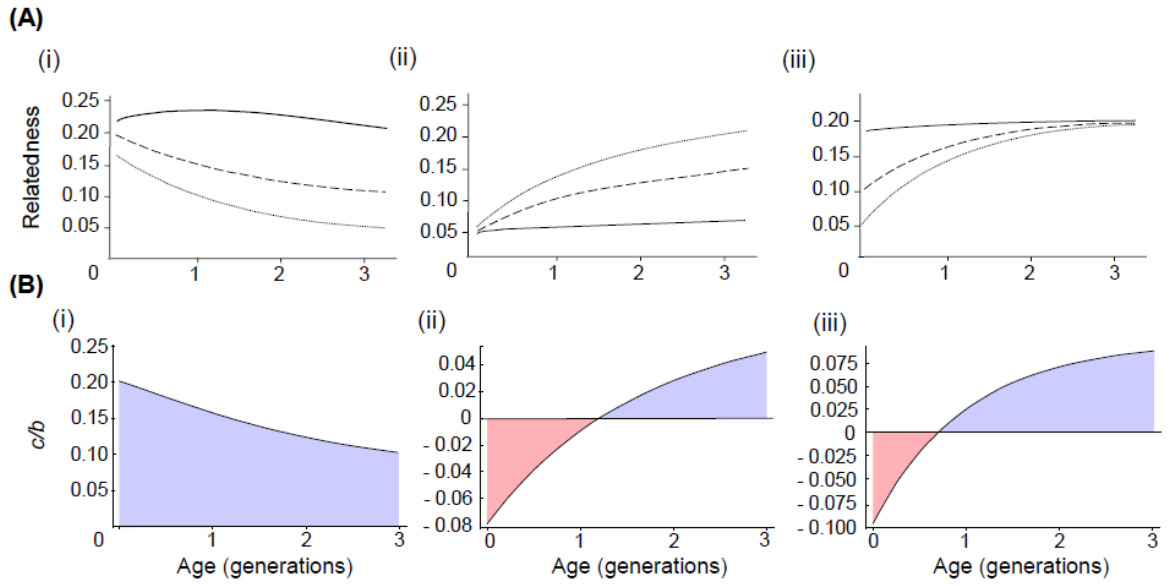
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795 Fig 2.

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