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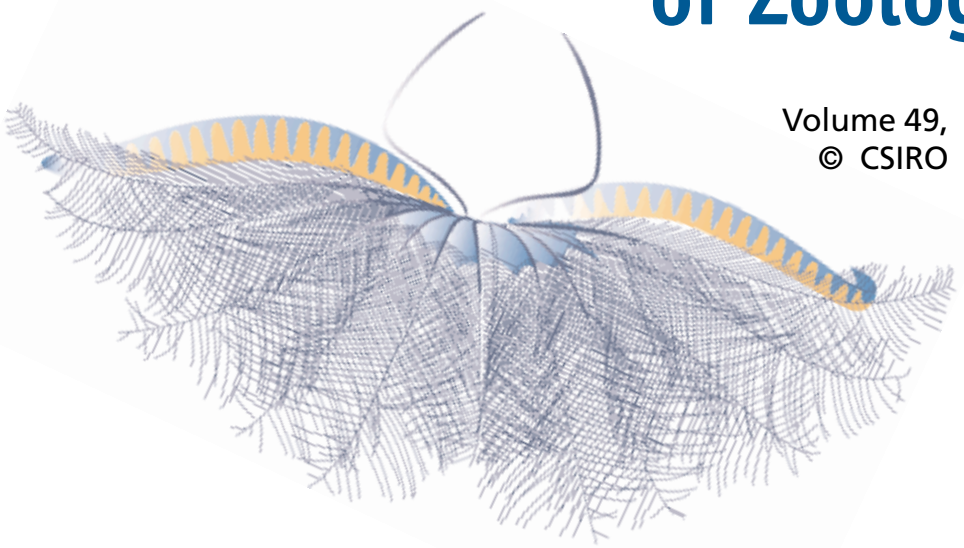

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Group size effects in quokkas

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Abstract

The amount of time allocated to vigilance, foraging, and locomotion as a function of group size were studied in the quokka (*Setonix brachyurus*), a small, moderately social, macropodid marsupial, on Rottnest Island. Despite living in isolation from most predators for up to 7000 years, quokkas exhibited typical group size effects of aggregation: they foraged more and showed less visual vigilance as group size increased. Group size effects, therefore, may result from factors other than antipredator benefits. In groups larger than 10, quokkas, uniquely among macropodids, allocated virtually all of their time to foraging and none to looking. Given virtually no predation risk on Rottnest Island and no antipredator benefit from aggregation, competition for food or other resources may also be important factors influencing time allocation in quokkas. Quokkas seemingly retained some apparent antipredator behaviour: they remained sensitive to the distance they were from cover and to the time of day when allocating time to foraging and looking.

Introduction

Many animals adjust the time they allocate to social and non-social behaviour as a function of group size. Such group-size effects are most often studied by examining the trade-off between time allocated to antipredator vigilance and foraging (Roberts 1996; Bednekoff and Lima 1998). Typically, individuals forage more and are vigilant less as group size increases and this finding is often attributed to a reduction in the *per capita* risk of predation as group size increases (Quenette 1990). However, the reduction in visual vigilance and increase in foraging need not result from a beneficial reduction in predation risk; scramble competition can also cause animals to forage more and be vigilant less as group size increases (Beauchamp and Livoreil 1997; Beauchamp 1998). What happens when a population becomes isolated from predators? Some evidence suggests that isolation from predators leads to the loss of group size effects (Catterall *et al.* 1992), but isolation may not affect all species similarly. As part of a comparative study on the evolution of group size effects in macropodids (kangaroos, wallabies and rat kangaroos), we studied quokkas (*Setonix brachyurus*), a small (2.7–4.2 kg), moderately social, macropodid marsupial (Kitchener 1995), and asked whether group size influences time allocation in a location where quokkas have not been exposed to significant predation for up to 7000 years.

Quokkas formerly ranged through much of south-western Australia, but are now endangered on the mainland (Kitchener 1995; Maxwell *et al.* 1996). They are the only native terrestrial mammal on the 1950-ha Rottnest Island, located 18 km off the Western Australia mainland (Abbott and Burbidge 1995). Rottnest Island was isolated by sea level changes about 7000 years ago (Playford 1983) and became, from the quokkas' perspective, virtually predator-free.

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Although three eagle species are occasionally recorded as vagrants (wedge tailed eagles, *Aquila audax*; little eagles, *Hieraaetus morphnoides*; sea eagles, *Haliaetus leucogaster*), may stay for several weeks, and may prey on the occasional quokka, no avian predators of quokkas are resident on the island. Two small snakes, the non-venomous and tiny southern blind snake (*Ramphotyphlops* sp.) and the venomous dugite (*Pseudonaja affinis*) are found on the island. Dugites reach a maximum of 1 m in length and forage primarily on mice. Both snakes are too small to prey on quokkas.

Since settlement in 1830, quokkas have been subjected to some predation by humans, which ceased early in the 20th century, and presumably low levels of predation by human-introduced feral cats (*Felis catus*). Now, quokkas on Rottnest Island are remarkably unresponsive to humans and are routinely described as 'tame'. The Dutch sailors who discovered and named the island 'Rott Enest' ('rats nest') were the first to note their 'tameness' and abundance. There is no evidence of Aboriginal occupation of the island prior to European arrival (Saunders and Rebeira 1989).

The objective of this study was to determine whether quokkas showed group size effects in their time allocation and to identify other factors that may influence the time that quokkas allocated to foraging and vigilance. We aimed to better understand how the loss of most of a species' predators influenced the relative benefit that individuals obtained by aggregation.

Methods

Subjects and study site

We studied free-ranging quokkas on and around the Rottnest Island golf course and around the Kingston youth hostel in December 1999. Quokkas at both locations were well habituated to humans. They spent their days resting in the shade of dense shrubs and emerged in the late afternoon or early evening to forage in the open.

General procedures

We video-recorded 5-min focal animal samples of animals between 17:45 and 23:15 hours on nights without rain or heavy wind. We stood or sat in locations where we did not detectably influence our focal subject's behaviour. On average, we observed quokkas from 9.8 m (±5.2 s.d.). In other studies we routinely observe quokkas at distances as close as 1 m without detectably affecting their natural behaviour.

We observed quokkas from the time when they moved out of cover to forage in the late afternoon. After sunset we affixed image intensifiers (ITT Nightcam 300) with 80–200-mm zoom camera lenses (Nikkor and Minolta) to the video cameras (Panasonic VX77A). We illuminated the image-intensified video field with a standard 1-W Petzl head lamp. Quokkas at one of our sites (Kingstown Barracks) were habituated to lights. For quokkas and other macropodids (Blumstein and Daniel, unpublished) we observed no obvious change in behaviour when animals were illuminated with the 1-W light.

Individuals were not captured or marked as part of this study, although some individuals were ear-tagged, micro-chipped, or fur-dyed from previous and on-going studies (McLean and Schmidt 1999). To avoid observing individuals more than once (i.e. to preserve statistical independence), we systematically walked through meadows and did not double-back on our paths. We did not re-sample the same area on more than one night. We are confident that the observations come from different individuals.

At the beginning of each focal sample we noted the following variables: the time of day (day/dusk/night, where dusk was defined as between 1 h before and 0.3 h after sunset); age (scored only when unambiguous as adult/sub-adult on the basis of size and morphology) and sex of the focal animal (scored only when positively identified); the distance of the focal animal to protective cover (quokkas returned to dense vegetation when alarmed); and the number of other conspecifics within 10 m and 50 m (solitary animals were scored as being in a group of 1).

A single person (JCD) scored videotaped focal animal samples using The Observer 3.0 (Noldus Information Technologies 1995), and noted the onset of each bout of foraging (included foraging on the ground and on shrubby vegetation and tree limbs above the ground), vigilance, and several other behaviours. Vigilance was divided into several categories: while crouching or standing (the onset of a bout was scored each time an individual moved its head and fixated), while rearing up (differentiated from

quadrupedal crouching and bipedal standing by the upright angle of the back). Other behaviours included: pentapedal walking (kangaroos and wallabies move their back legs forward while balancing on their forepaws and tail), hopping, grooming, affiliative behaviour (e.g. sniffing and allogrooming), and aggressive behaviour (displacement, chase, box). We also noted when animals went out of sight and when they were back in sight.

From the video record we calculated the percentage of time allocated to each behaviour out of the total time the animal was in sight. We combined our two measures of vigilance (crouching or standing and rearing up) to generate one behaviour, vigilance. Pentapedal walking and hopping were combined to form a new behaviour, locomotion. These analyses focus on the three most common quokka behaviours – foraging, vigilance, and locomotion.

Statistical analysis

We used the individual as the unit of analysis. Statistical analyses were conducted using Statview 5.0 (SAS Institute 1998) and SPSS 10 (SPSS Inc. 2000).

To study group size effects, we fitted linear and logarithmic models to the proportion of time in sight allocated to vigilance, foraging and locomotion. We averaged the time allocations for all observations of quokkas observed at a given group size, defining group size two ways: the total number of quokkas within 10 m and 50 m. We assumed that the model that explained the most variation reflected how quokkas assessed group size.

We fitted non-parametric ANOVA models (followed up by *post hoc* Mann–Whitney *U*-tests with the *P*-value adjusted to reflect multiple comparisons) to study how distance to nearest cover (split into four distance categories: 0–1 m, 2–10 m, 11–50 m, and >50 m) influenced time allocation, and whether the time of day (day, dusk, night) influenced time allocation. Mann–Whitney *U*-tests were used to check for the effects of age and sex on time allocated to vigilance, foraging and locomotion.

Following bivariate analyses, we fitted random-factor ANCOVA models (using SPSS) that included those factors that significantly explained variation in time allocation (distance to cover and time of day) along with group size (defined as the number of conspecifics within 10 m) as a covariate. To reduce the number of empty cells, we consolidated categories for distance to cover (≤10 m, >10 m) and time of day (day, dusk, night). These consolidations were justified because there were no significant differences within, but there were significant differences between, these new categories.

Results

We conducted focal animal samples on 128 quokkas. Of these, eight were excluded from subsequent analysis due to poor quality (we were unable to accurately or consistently distinguish between behaviours – for example, the focal subject had its back to the observer). Of the remainder, 92 were positively identified as adults (12 positively identified males, 28 positively identified females) and 14 were positively identified subadults. For each 300-s focal animal sample, the focal quokka was in sight an average of 280 s (±37 s.d.).

Group size defined as the number of quokkas within 10 m explained more variation in the time allocated to foraging and vigilance than did group size defined as the number of conspecifics within 50 m (Fig. 1). For groups defined as the number of conspecifics within 10 m, linear models explained as much or more variation than logarithmic models in the time quokkas allocated to foraging (group size defined as the number of conspecifics within 10 m: linear Adj. $R^2 = 0.605$, $P = 0.005$; logarithmic Adj. $R^2 = 0.517$, $P = 0.012$; group size defined as the number of conspecifics within 50 m: linear Adj. $R^2 = 0.287$, $P = 0.028$; logarithmic Adj. $R^2 = 0.340$, $P = 0.017$), vigilance (group size defined as the number of conspecifics within 10 m: linear Adj. $R^2 = 0.614$, $P = 0.004$; logarithmic Adj. $R^2 = 0.495$, $P = 0.014$; group size defined as the number of conspecifics within 50 m: linear Adj. $R^2 = 0.237$, $P = 0.044$; logarithmic Adj. $R^2 = 0.278$, $P = 0.031$), and locomotion (group size defined as the number of conspecifics within 10 m: linear Adj. $R^2 = 0.340$, $P = 0.045$; logarithmic Adj. $R^2 = 0.333$, $P = 0.047$; group size defined as the number of conspecifics within 50 m: linear Adj. $R^2 = 0.246$, $P = 0.041$; logarithmic Adj. $R^2 = 0.294$, $P = 0.026$).

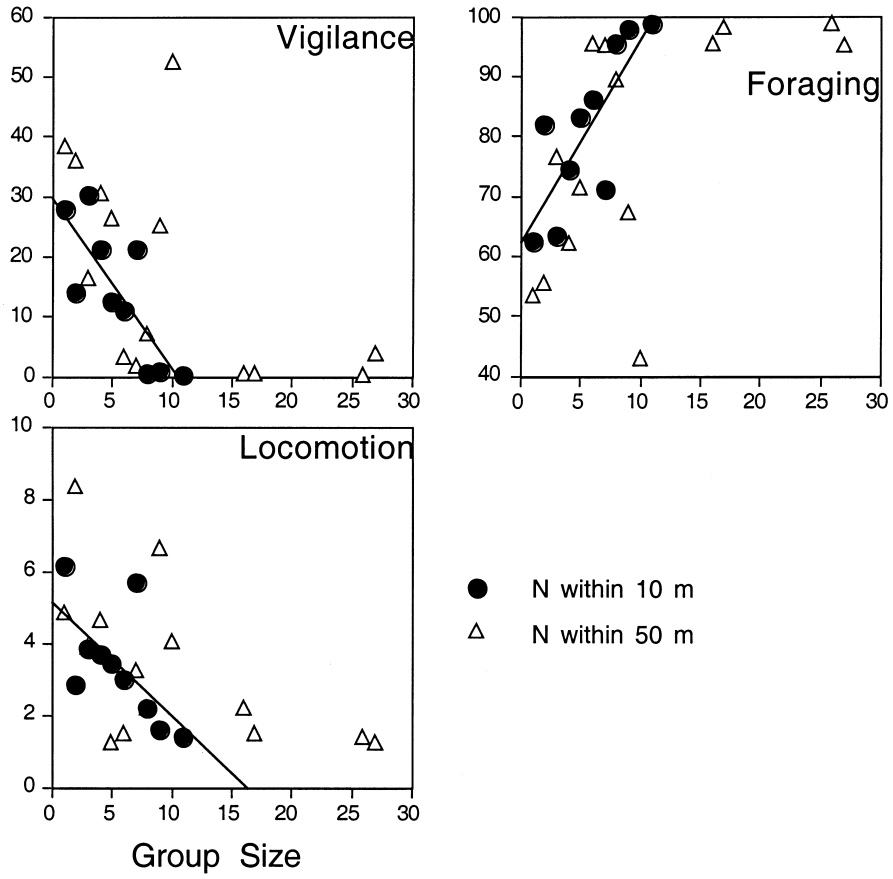

Fig. 1. The average percentage time that quokkas allocated to foraging, vigilance, and locomotion as a function of the number of conspecifics within 10 m (●) and 50 m (△). For all behaviours, group size defined at 10 m explained more variation than group size defined at 50 m, and linear regression models explained more variation than logarithmic regressions when group size was defined as the number of conspecifics within 10 m.

In addition to group size, time allocated to foraging and vigilance, but not locomotion (Kruskal–Wallis $P = 0.220$), varied as a function of the distance from cover: quokkas foraged more (Kruskal–Wallis $P < 0.0001$) and were visually vigilant less (Kruskal–Wallis $P < 0.0001$) when in the open (Fig. 2). Similarly, time of day influenced patterns of vigilance (Kruskal–Wallis $P = 0.0018$), foraging (Kruskal–Wallis $P = 0.0003$), and locomotion (Kruskal–Wallis $P = 0.0273$): quokkas foraged more (Mann–Whitney *U*-test, $P = 0.0009$), were less vigilant (Mann–Whitney *U*-test, $P = 0.0032$), and moved less at night than either during the day or at dusk (Mann–Whitney *U*-tests: forage: night *v.* day, $P = 0.0007$; night *v.* dusk, $P = 0.0021$; vigilance: night *v.* day, $P = 0.0016$; night *v.* dusk, $P = 0.0098$; locomotion: night *v.* day, $P = 0.0678$; night *v.* dusk, $P = 0.0155$; Fig. 3). Neither age, nor sex significantly explained variation in the time allocated to visual vigilance (Mann–Whitney *U*-tests: age, $P = 0.146$; sex, $P = 0.479$), foraging (age, $P = 0.185$; sex, $P = 0.461$), or locomotion (age, $P = 0.566$; sex, $P = 0.345$).

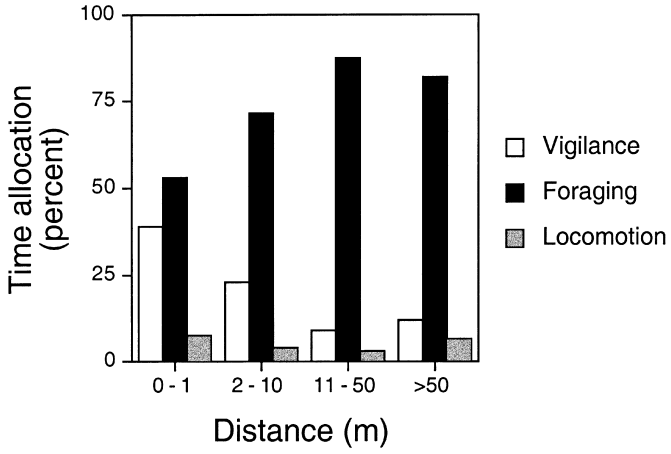

Fig. 2. The percentage time that quokkas allocated to vigilance (no fill), foraging (dark fill), and locomotion (grey fill) as a function of the distance to cover. Foraging and looking by quokkas was significantly influenced by distance from cover. *Post hoc* Mann–Whitney *U*-tests (*P*-critical 0.05/6 = 0.0083) suggest that quokkas forage more and look less when 11–50 m from cover than they do when 0–1 m and 2–10 m from cover.

The final ANCOVA models contained group size, time of day, distance to cover and the interaction between time of day and distance to cover. Group size, but no other main effect (all $P > 0.355$) explained significant variation in the time allocated to foraging ($P = 0.012$) and vigilance ($P = 0.016$), but not locomotion ($P = 0.189$). There were significant interactions between time of day and distance to cover for foraging ($P = 0.021$), vigilance ($P = 0.026$) and locomotion ($P = 0.050$).

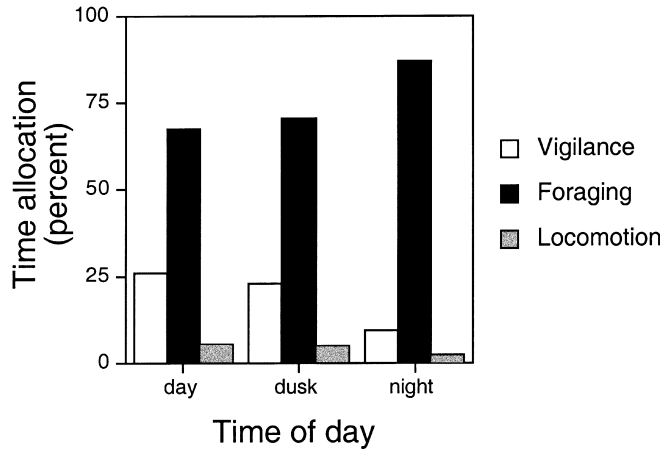

Fig. 3. The percentage time that quokkas allocated to vigilance (no fill), foraging (dark fill), and locomotion (grey fill) as a function of time of day. *Post hoc* Mann–Whitney *U*-tests (*P*-critical 0.05/3 = 0.017) suggest that quokkas forage more and look less at night than during the day or at dusk, and move less at night than at dusk.

Discussion

Taken together, these results suggest that time allocation by quokkas was primarily influenced by group size. Bivariate analyses suggested that quokkas foraged more and were less vigilant at night when farther from cover and when surrounded by more conspecifics. Group size and time of day affected locomotion. However, the results from the ANCOVA models suggest that, after controlling for variation accounted for by time of day and distance to cover, group size alone explained significant variation in the time that quokkas allocated to foraging and vigilance.

Like other small macropodids (tammar wallabies (*Macropus eugenii*): Blumstein and Daniel, unpublished; and yellow-footed rock-wallabies (*Petrogale xanthopus*): Blumstein *et al.* 2001), quokkas perceived those relatively spatially close conspecifics as group members; group size defined as the number of conspecifics within 10 m explained more variation than group size defined as the number of conspecifics within 50 m. However, 9% more variation in foraging, 12% more variation in looking, and 1% more variation in locomotion was explained by linear than by logarithmic models.

Three models of predation hazard assessment ('dilution' – Hamilton 1971; 'detection' – Pulliam 1973; 'security' – Dehn 1990) predict nonlinear functions for antipredator vigilance and foraging. This effect is easiest to envision by considering the risk to a solitary individual joined by at first one, then two other conspecifics. Assuming that a predator takes only one prey, the solitary individual's risk of predation is half that of being alone if associating with one other individual, and one third that of being alone if associating with two other individuals. Detection and security-effect models also predict a similar nonlinear relationship between group size and predation risk, and therefore between group size and time allocated to vigilance and foraging.

Group size effects offer benefits to individuals, but aggregation may also have costs. For instance, interference competition can reduce the time allocated to foraging and/or feeding rate as group size increases (Clark and Mangel 1986; Beauchamp 1998; Blumstein *et al.* 2001).

The interaction between beneficial and costly aspects of aggregation will be reflected in the specific shape of the function. Assuming that predation risk influences time allocation, the addition of interference competition will modify the group size function, driving the curve away from its initial positively curvilinear form (see Blumstein *et al.* 2001 for a detailed discussion). The final shape of the relationship will be determined by the relative strengths of these two effects. Linear group size functions suggest that interference competition is reducing the benefits that animals obtain by aggregating to reduce predation risk.

Quokkas in groups of about 10 or more allocated virtually all their time to foraging and eliminated vigilance, as measured over a five-minute period (Fig. 1). In contrast, none of the other species of kangaroos (*Macropus giganteus* – Heathcote 1987; Jarman 1987; Jarman and Wright 1993; Payne and Jarman 1999; *M. fuliginosus* – Coulson 1999; Blumstein and Daniel, unpublished) or wallabies (*M. eugenii* – Blumstein *et al.* 1999; Blumstein and Daniel, unpublished; *M. rufogriesus* – Coulson 1999; *Petrogale xanthopus* – Blumstein *et al.* 2001) in which group size effects have been studied allocated all their time to foraging after some threshold group size had been exceeded. It is important to emphasise that the absence of virtually all predators on Rottnest Island means that non-vigilant quokkas had no higher rate of predation than vigilant ones. Thus, there was little benefit to antipredator vigilance. If anything, there may have been selection against antipredator vigilance because vigilant quokkas had less available time to forage.

An alternative perspective is that vigilance in quokkas may not be an antipredator behaviour: perhaps there is no need to be vigilant if there are no predators. Male quokkas spend much of their time in short-term liaisons with females (McLean *et al.*, unpublished). At the time of this study, many female quokkas had dependent young, and could have been looking out for them. Also, breeding was just beginning, so males were watching for each other and females may be watching for males who harass them continually (McLean and Schmitt 1999; McLean *et al.*, unpublished). Thus, the primary function of vigilance could be to monitor conspecifics (social vigilance: Roberts 1988). However, if vigilance were primarily social, time allocated to vigilance should probably increase with group size; we observed the opposite.

Scramble competition, alone, may explain group size if individuals forage more or at a higher rate because of perceived competition over an exploitable resource (Elgar 1989). The addition of group members led to an initial increase in the time quokkas allocated to foraging; a finding consistent with the scramble competition hypothesis. However, if scramble competition alone explained observed group size effects, we would predict that foraging by quokkas would not be sensitive to other factors related to perceived predation risk. Bivariate analyses and the significant interaction between time of day and distance to cover in the ANCOVA models suggest that quokkas remained sensitive to the distance they were from cover and to the time of day when allocating time to foraging and looking. We speculate that quokkas retained some degree of antipredator behaviour and seek an explanation for group size effects that includes both competition and variation in predation risk.

It is possible that an interaction of interference competition with the perceived antipredator benefits of aggregation, which appears to have persisted despite up to 7000 years of relaxed selection, is responsible for the observed linear group size effect. Interference competition reduces the time allocated to foraging with increased group size and can modify the group size × time allocation function, making it linear.

Regardless of the mechanism of competition, some studied species isolated from their predators are less vigilant than those with predators (Hunter and Skinner 1998) and may lose group size effects (Catterall *et al.* 1992). For instance, an insular population of western grey kangaroos living with limited risk of predation did not exhibit the group size effects found in a mainland population living under the threat of predation (Blumstein and Daniel, unpublished). However, isolation from predators may not only modify vigilance and remove group size effects, it may also release competition that may be suppressed when predators are present.

Much as the presence of predators influences patterns of interspecific competition (e.g. Paine 1966; Kotler 1984), the removal of predators or variation in predation risk may also influence the importance or expression of intraspecific competition (but see Grand and Dill 1999). Quokkas have dominance hierarchies that determine patterns of access to water and shelter (Kitchener 1995) and influence access to mates (McLean and Schmidt, unpublished). Perhaps these social dynamics are facilitated by life on a predator-free island.

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