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Fitness increases with partner and neighbour allopreening

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Altruism and selfishness are fundamental characteristics of human and animal societies. Among colonial biparental species, breeding outcome depends on interactions between mates and neighbours. However, the relationships between cooperation within and among partnerships and fitness have not been fully investigated. We show that in the highly colonial common guillemot (*Uria aalge*), altruistic behaviour (allopreening) towards a mate was positively related to long-term fitness, whereas allopreening a neighbour was related to current fitness. Turnover is much lower within than between pairs, so our results suggest that allopreening within pairs generates fitness returns at longer timescales than between pairs. Allopreening not only removes ectoparasites and maintains plumage condition, but may also have important social functions. We found a negative relationship between fight rate and allopreen rate between breeding neighbours, with nests exhibiting low breeding success having a higher frequency of fights with neighbours. We also found evidence for reciprocity in allopreening. Thus, allopreening may function as a reciprocal stress reducer, to decrease the likelihood of fights and associated breeding failure. We suggest that altruistic behaviour has long-term benefits for the survival of the offspring when living in a crowded neighbourhood.

Keywords: altruism; allopreening; parental care; conflict; neighbours

1. INTRODUCTION

A fundamental question in sociobiology is the evolution of cooperation and altruism in humans and other species (Hamilton 1964; Trivers 1971; Axelrod & Hamilton 1981; Fehr & Fischbacher 2003). Among monogamous species with biparental care, cooperation may be a key determinant of fitness (Black 1996). In colonial species, cooperation among breeding neighbours is also likely to be important. However, few studies have examined how cooperation within and between pairs operates and how this relates to breeding

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success, particularly given the marked skew in fitness across individuals (Newton 1985).

Allopreening, where one individual bird preens another (Harrison 1965), is a useful behaviour to study in the context of understanding cooperation and altruism because it involves an individual actively helping its mate or neighbour (as opposed to working for the direct benefit of offspring). Despite the widespread occurrence of allopreening among bird species (Harrison 1965), its functions are poorly understood. The analogous behaviour of allogrooming in mammals is often interpreted as an example of reciprocal altruism (Seyfarth & Cheney 1984; Hart & Hart 1992). The hypothesis that reciprocity acts as a mechanism maintaining altruism (Trivers 1971) has attracted much theoretical interest (Axelrod & Hamilton 1981; Roberts & Sherratt 1998). Whether individuals allopreen to invoke a reciprocal response or to benefit directly from preening others, two general functions of allopreening have been put forward (Radford & Du Plessis 2006). Hygiene, in particular ectoparasite removal and plumage maintenance, is viewed as a key function because allopreening is typically concentrated on areas of the body that individuals cannot reach (Clayton 1991). However, there is growing evidence that allopreening has important social functions. Among species that live in hierarchical groups, dominant individuals receive more allopreens than subordinates (Radford & Du Plessis 2006). Social functions may also be important in socially monogamous, colonial species. Allopreening may function to reaffirm the pair bond after separation (Black 1996). If time spent allopreening is limited by other demands, then it may also be important in mate choice as an honest signal of quality (Zahavi 1975; Roberts 1998) or used in assessing a potential mate (Stopka & Graciasova 2001), for example, by determining ectoparasite load. Alternatively, individuals may preen their partners to encourage parental care. Allogrooming may stimulate hormone production (Keever *et al.* 1989), including prolactin which promotes parental care (Buntin 1986). Finally, allopreening may reduce stress (Terry 1970) resulting in a reduction in aggression.

As these functions are not mutually exclusive, the relationship between allopreening and fitness is likely to be complex. Furthermore, among colonial species, an individual may gain a fitness benefit from preening both its mate and breeding neighbours. However, the dynamics of allopreening may operate at different timescales since the duration of relationships may differ. Among many long-lived species, turnover of neighbours is greater than mates, because individuals are more likely to move than they are to divorce (Black 1996). Thus, mate allopreening may generate fitness returns at longer timescales than neighbour allopreening.

We examined the relationship between allopreening and fitness in a highly colonial, cliff-nesting bird species (the common guillemot, *Uria aalge*). Guillemots exhibit biparental care and are socially monogamous with low divorce rates (Kokko *et al.* 2004). Despite this stability in their immediate social environment, they breed at very high density in physical contact with breeding neighbours, and turnover between pairs is high (Kokko *et al.* 2004). They lay a single egg directly on the cliff ledge and elevated levels of aggression and

Table 1. Possible functions of allopreening in socially monogamous, colonially breeding species, including fitness benefit, recipient, predicted relationships with preen rate and which were tested in this study (see electronic supplementary material). (Note that other functions have been put forward in species that live in hierarchical cooperatively breeding groups (reviewed in Radford & Du Plessis 2006).)

function	fitness benefit	recipient	prediction	tested	reference
1. reciprocity	to be preened in return to benefit self, e.g. parasite removal, feather maintenance, stress reduction (see below)	mate/neighbour	positive correlation between preen rates of players	yes	Seyfarth & Cheney (1984); Hart & Hart (1992)
2. parasite removal/feather maintenance	to improve condition of mate or breeding neighbour (reduces offspring predation if neighbouring pairs breed successfully)	mate/neighbour	negative/positive correlation between preen rate and parasite load/feather condition	no	Clayton (1991); Hart & Hart (1992)
3. mate choice (signalling and assessment)	preening as a sexually selected honest signal of quality; as means of assessing quality of potential mate	mate	positive correlation between preen rate and mate selection	no	Zahavi (1975); Roberts (1998); Stopka & Graciasova (2001)
4. pair-bond maintenance	preening as ritualized behaviour to reaffirm pair bond after prolonged separation	mate	positive correlation between preen rate and length of the pair bond	yes	Black (1996)
5. stress reduction	tactile stimulus to reduce stress levels and aggression	mate/neighbour	negative correlation between fight rate and preening rate	yes	Terry (1970); Feh & Demazieres (1993)
6. parental care stimulation	to promote production of hormones such as prolactin that encourage care	mate	a) positive correlation between preen rate and hormone levels; b) positive correlation between preen rate and care	no	Buntin (1986); Keverne <i>et al.</i> (1989)

fighting between pairs frequently result in the loss of eggs or young (Birkhead 1978). Guillemots are infested with the seabird tick *Ixodes uriae* (Barton *et al.* 1996). Allopreening of mates and breeding neighbours is one way and is directed towards parts of the body inaccessible to self-preening (typically the head and neck), with individuals taking it in turns to preen each other. Thus, both hygiene and social functions of allopreening may be operating, and reciprocal altruism may be occurring both within and between pairs. Our study had two main aims: (i) to test whether allopreening rates within and between neighbouring pairs are positively related to fitness, and determine over what temporal scale of fitness do any relationships operate and (ii) to examine the functional link between allopreening and fitness (table 1).

2. MATERIAL AND METHODS

The study was carried out on the Isle of May, Firth of Forth, Scotland (56°11' N, 2°33' W; 18 858 pairs in 2005), where individually marked guillemots have been studied since 1984. Incubation lasts approximately 34 days and the chick spends a further approximately 21 days in the colony, and mates alternate duties throughout incubation and chick brooding (Wanless & Harris 1986). The study group consisted of 33 pairs in which one or both members were colour ringed. The sex of each ringed bird was known from behavioural observations (Wanless & Harris 1986). Average pair-bond duration was 4.94 ± 5.07 years, whereas neighbour relationships were on average 1.56 ± 2.13 years.

We compared allopreening rates with a long-term measure of fitness (average breeding success in the time the pair had bred together) and a short-term measure (current breeding outcome: zero or one chick fledged).

Each site was monitored from dawn to dusk throughout incubation. A video camera system (<http://www.tracksys.co.uk/index.php>) recorded study nests, from which within-pair allopreening rates were quantified. Neighbour allopreening and fight rates were recorded at 10 pairs that had neighbours within pecking distance (see electronic supplementary material).

We used linear mixed models, generalized linear mixed models and correlations to analyse relationships (see electronic supplementary material for full details).

3. RESULTS

We found a significant positive relationship between long-term fitness and the rate of allopreening within a pair (Wald statistic $W=6.44$, d.f.=1, $p=0.011$; figure 1). However, there was no relationship between current fitness and mate preen rate ($W=0.03$, d.f.=1, $p=0.9$). There was a marked difference between the sexes with males preening partners significantly more than females (males = 1.419 ± 0.56 and females = 1.010 ± 0.47 preens min^{-1} ; $W=7.14$, d.f.=1, $p=0.008$; table 1). Allopreening of neighbours was related to current fitness, with those pairs that preened their neighbours at a higher rate having a higher breeding success ($W=4.04$, d.f.=1, $p=0.044$; figure 2), but no effect on long-term fitness ($W=0.04$, d.f.=1, $p=0.8$). There was no difference

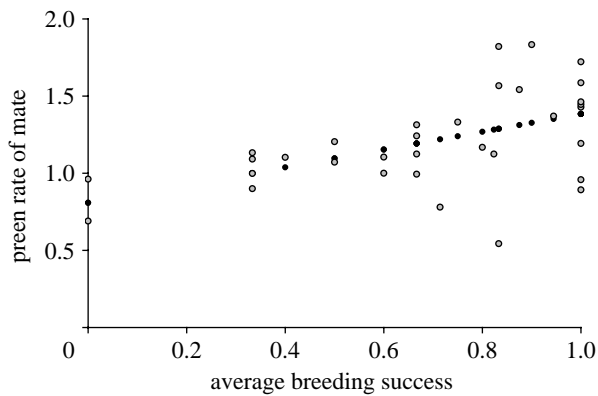


Figure 1. Relationship between average rate of preening a mate (from the number of preens min^{-1}) during change-overs between incubation shifts and the average breeding success for 33 pairs of guillemots.

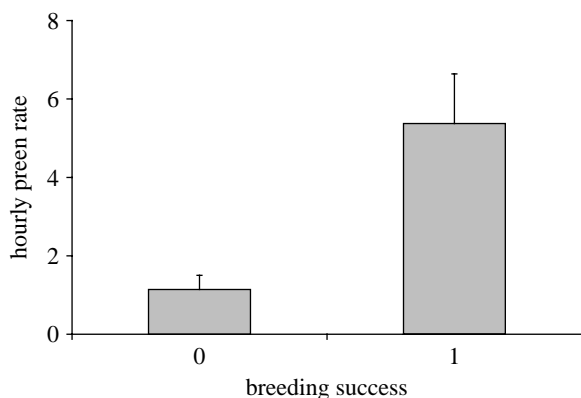


Figure 2. Relationship between average rate (+s.e.) of preening neighbour (from the number of preens h^{-1}) and breeding success, during day-long observations of nest sites with neighbours ($n=10$).

in the rate at which males and females preened neighbours, and the sex of the recipient had no significant effect on preen rate (sex of preener: $W=0.05$, d.f.=1, $p=0.8$; sex of recipient: $W=0.23$, d.f.=1, $p=0.6$). No interactions were significant in either model. The average allopreening rate within and between pairs was not correlated ($r=0.09$; $p=0.74$).

We found no evidence for the pair-bond maintenance function (length of the pair bond fitted to the above model on pair preen rate: $W=0.32$, $p=0.6$). However, there was a significant negative correlation between the average rate of preening between the nests and number of fights observed ($r=-0.825$; $p=0.006$). Furthermore, there was a significant negative association between the number of fights and breeding success ($W=8.15$, d.f.=1, $p=0.004$), but no effect of initiator sex ($W=1.68$, d.f.=1, $p=0.2$) or neighbour sex ($W=1.21$, d.f.=1, $p=0.3$). Failures at nests where preening frequencies between neighbours were lower occurred as a direct result of a fight in which either the egg or chick was displaced (see video in electronic supplementary material) or was deliberately thrown off the ledge.

There was evidence for reciprocity between breeding neighbours (significant positive relationship between preen rates, $W=24.05$, $p<0.001$), but not within pairs ($r=-0.28$, $p=0.11$).

4. DISCUSSION

Guillemots are long-lived and exhibit high levels of mate and site fidelity (Kokko *et al.* 2004). Turnover of neighbours is typically greater than mates and so, on average, associations between members of a pair last longer than those between neighbours. These differences in the duration of interactions within and between pairs may result in functions for allopreening that generate returns at different rates. For guillemots, the rate at which an individual grooms its mate is linked to fitness measured over a longer timescale, in association with the much greater likelihood that the relationship will persist across years. This longer timescale may explain why we found no evidence for reciprocity in preen rate within pairs. In contrast, the function of allopreening of neighbours is linked to fitness in the current breeding attempt. Our results suggest that this may be due to the need to minimize egg or chick loss during fights, since fight rate was negatively related to preen rate and aggression between neighbours was lower in pairs which were successful. We also found evidence of reciprocity between neighbours, which accords with preen rate of neighbours functioning to benefit current rather than long-term fitness. Our results therefore suggest that allopreening of neighbours serves as an important reciprocal stress reducer (Terry 1970; Feh & Demazieres 1993).

The removal of ectoparasites such as *Ixodes* ticks and plumage maintenance may also be important functions of allopreening in guillemots, since ticks are generally found in the region of the head and neck, where allopreening is concentrated (Barton *et al.* 1996). We found little evidence of the function of allopreening in pair-bond maintenance, but it may be important in mate choice (Roberts 1998). The higher allopreening rate of males accords with a study of herb-field mice *Apodemus microps* (Stopka & Graciosa 2001), where there is a discrepancy in mating opportunities between the sexes, with allo-grooming suggested as a method of signalling and assessing potential mates. However, in biparental species such as guillemots, mate choice and same-sex competition is likely to be operating in both sexes (Jones & Hunter 1993). In guillemots, females exhibit higher chick feeding rates than males (Wanless & Harris 1986). Thus, it is possible that males preen females more during incubation to stimulate production of care-promoting hormones such as prolactin (Buntin 1986).

Our results suggest that, in a crowded neighbourhood, allopreening is an important altruistic behaviour that has multiple functions at different fitness scales. Understanding how cooperation between pairs and neighbours correlates with breeding success is important in interpreting the costs and benefits of coloniality.

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