

Forum

Ideal flea constraints on group living: unwanted public goods and the emergence of cooperation

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Long ago, Hamilton (1971) proposed that the “selfish herd” effect, while primarily thought to reduce predation risk, might also apply to avoiding parasites. Solitary individuals suffer higher ectoparasite burdens if they lack conspecifics either to absorb collateral damage from the local ectoparasite population or to remove ectoparasites by allogrooming. By grouping, therefore, animals may reduce their individual risk of exposure to parasites (Mooring and Hart, 1992). This is important because there are significant fitness costs associated with ectoparasite loads. More ectoparasites take more blood, cause more irritation, increase the probability of infection, and decrease the time available for other activities, because grooming becomes a higher priority. These costs vary with group size because a greater number of hosts and shared den sites means ectoparasites are more likely to survive stochastic variation. The dynamics of parasite control might therefore

present crucial constraints on group size and a novel origin for sociality itself.

We present a model suggesting that these constraints may lead to an egalitarian system among social host species, who need to cooperate to get rid of their ectoparasites. Mobile ectoparasites are moderated by two mechanisms: (1) the dilution of ectoparasites toward an ideal free distribution (IFD) among hosts, and (2) the removal of ectoparasites by cooperative host allogrooming. Host interactions represent a “biological market,” in which the benefit of cooperation varies with the relative amount of the tradable commodity (the ectoparasites) each individual has. This is not, however, a normal market as the goods are unwanted. Nevertheless, the dilution effect means that all individuals in a group have a common stake in reducing the mean parasite burden, which may preclude or reduce any advantage of cheating. Predictions of the model were tested with empirical data from a long-term study of badgers, *Meles meles*, and their flea burdens in Wytham Woods, Oxford.

A basic tenet in models of population dynamics (Hanski, 1999; Sutherland, 1996) is IFD, a general explanation for fluctuating distributions of animals as they move to find sites where the rewards are highest and individuals optimize their fitness (Fretwell, 1972; Fretwell and Lucas, 1970). Assuming individuals really are free (i.e., no resource defense and perfect information), this represents a process whereby consumers become diluted among all available sites. In short, the ratio between the numbers of individuals in sites A and B should be proportional to the relative availability of resources

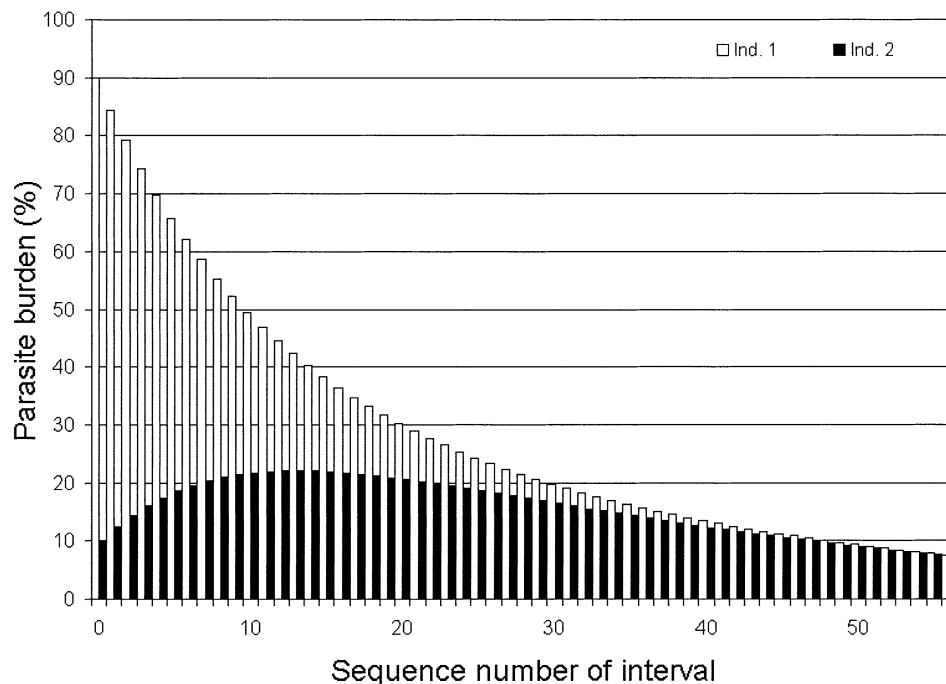


Figure 1

Bars represent the flea burden for two individuals over an arbitrary sequence of interactions. Flea burdens tend to an equilibrium between the two host individuals due to (1) dilution by ideal free distribution of fleas and (2) the increased success rate in grooming a more heavily burdened individual. The initial increase in the parasite load incurs a temporary increase in cost for the individual with a lower flea burden at T_0 . But repetition of this process in a group of individuals yields a tendency to equalize parasite loads and to decrease the overall burden. The speed of the process depends on the probability of encounters and on the distribution and the mean length of allogrooming bouts.

in sites A and B (Earn and Johnstone, 1997). Ectoparasites, as any other organism, are expected to tend to an IFD because they should distribute themselves among their hosts such that individual fitness is the maximum possible (given the behavior of all other conspecifics). We use a stochastic simulation to show that, in approximating to an IFD, the dynamic distribution of a mobile ectoparasite (flea) can favor social cohesion and cooperation behavior in its host.

Ectoparasites' exploitation of hosts is not tolerated passively. Host species act to reduce their ectoparasite burden by removing fleas, which impacts on ectoparasites in two ways: (1) a direct predation effect in that the hosts remove fleas by grooming themselves (autogrooming) (Geyer and Kornet, 1982; Mooring and Samuel, 1998), and (2) an indirect predation effect in that *social* hosts can cooperate to groom each other (allogrooming). This significantly improves ectoparasite removal as they can be removed from places that a single host cannot physically reach via self-grooming (Hart and Hart, 1992; O'Brien, 1993; Stewart, 1997; Stopka and Graciasová, 2001).

These features make the system amenable to a model that combines the principles of IFD and biological markets (Noë and Hammerstein, 1995), reflecting two interacting dynamics. Fleas tend toward IFD, but hosts' willingness to come into contact with each other is mediated by the strategic consequences of two potential exchanges:

1. Dilution effects will differentially affect different individuals (those with many fleas may off-load some, but those with few gain more). So hosts may passively *exploit* the effects of ectoparasite IFD if they have the larger parasite burden in a dyad. Conversely, if they have a lower burden, they *suffer* from dilution effects.
2. The opportunity to trade cooperative allogrooming can reduce the mean parasite burden of both allogroomers (remembering that in coming into contact they experience dilution effects as well).

Hosts are presented with a game theoretical problem of whether to cooperate or not. Both dilution and grooming present strategies for a host to minimize their ectoparasite burden, but both depend on the other individuals' predicament so the resulting dynamics are not obvious without simulation.

A simulation model

Model description

To determine the consequences of these dynamics, we simulated how different efficiencies of dilution and grooming would impact on (1) the underlying tendency toward IFD; (2) the potential for cooperation among hosts; and (3) optimal host group sizes.

We described above how two interacting individuals should experience a change in their flea loads owing to both migration of fleas and allogrooming. Figure 1 illustrates how, over a series of repeated interactions within the same pair, each individual's flea load approaches an equal amount (due to migration) and, in addition, their absolute flea loads diminish over time (due to grooming). We used simulations to examine this process as it occurs in multi-individual groups and, in particular, how it varies among different group sizes, different rates of migration, and different efficiencies of grooming.

To do this, we assigned individuals in hypothetical groups an ectoparasite load drawn from exponentially distributed random numbers. Subsequently, all individuals within such a group came into contact with a randomly assigned partner (always from within the same group). During contact between any two individuals, fleas could migrate from one individual to

another (and vice versa), and were also removed by allogrooming each other. A pair of individuals interacted just once (i.e., they experienced one instance of both migration and of allogrooming between them) before being reshuffled and assigned a new random partner (they were not excluded from meeting each other again). The simulations continued until each individual had experienced 100 interactions. For each group size, our model had two parameters: the efficiency of allogrooming (α , given by the fraction of fleas removed per unit time) and migration rate (β , the fraction of fleas which swap hosts in an interaction). These fractions (for both α and β) could be set at either of two levels: 1/1000th when "low," and 1/10th when "high" (simulations with all four possible combinations were compared). The results of the simulations (Figure 2) are given as the mean of 100 different runs per each group size (and per each combination of α and β). In each run, the simulation was started with fresh individuals.

Over several interactions, migration gradually led to an equalization or "dilution" of the parasite loads among all individuals in the group (a multiplayer version of Figure 1), independent of whether the total number of fleas involved changes or not (as a result of removal by grooming). Thus, variance in parasite loads among the hosts diminishes, whereas the total number is in continual decline due to allogrooming. As time tends to infinity both the variance and the total number tends to zero.

Model results

Given two states of each parameter ($\alpha_1, \alpha_2, \beta_1, \beta_2$), a matrix of four scenarios can be depicted as in Figure 2. Each panel of Figure 2 shows the results of stochastic simulations showing *rates of change* among group members in mean flea burden (white bars) and flea burden variance (black bars) for various group sizes. The values for each state of migration rate and grooming efficiency ($\alpha_1, \alpha_2, \beta_1, \beta_2$) are arbitrary and simply represent low and high values of each parameter. These ignore any fluctuations in flea reproduction or immigration from underground dens, so the simulations should be considered as single nights, during which flea burdens are altered only by host behavior.

Figure 2 leads to the following conclusions. (1) When individuals do not allogroom and their fleas do not migrate either (lower right panel), the speed of change in the mean and the variation is constant at zero. (2) When fleas migrate but individuals do not allogroom (lower left), the variation in number of fleas changes most rapidly in small groups but the mean remains constant. (3) When allogrooming is high and migration rate of fleas is high (upper left), it is advantageous for any individual with a high parasite load to enter a small group in which the mean and variation changes rapidly. (4) Animals that allogroom but with ectoparasites that do not migrate (upper right) can also profit from being in small groups: individuals entering the group with a high parasite load still profit from allogrooming. (5) Whether fleas move or not (the difference between the upper panels), if hosts allogroom in a reciprocal fashion that maintains a similar duration of allogrooming given and received (simplified Tit for Tat [TFT] or "parcelling" [Connor, 1995]), the mean changes as rapidly as the variation of fleas per individual. The distribution of fleas, therefore, gradually equalizes between all individuals, leading to an IFD of parasites over the landscape of potential hosts. In terms of minimizing ectoparasites, these results indicate a strong selective pressure against solitary living and, at the other extreme, some limit on the benefit of very large groups.

The model presented above provides specific predictions that can be tested: (1) parasite dilution should occur more rapidly in smaller groups, in which there are larger changes in

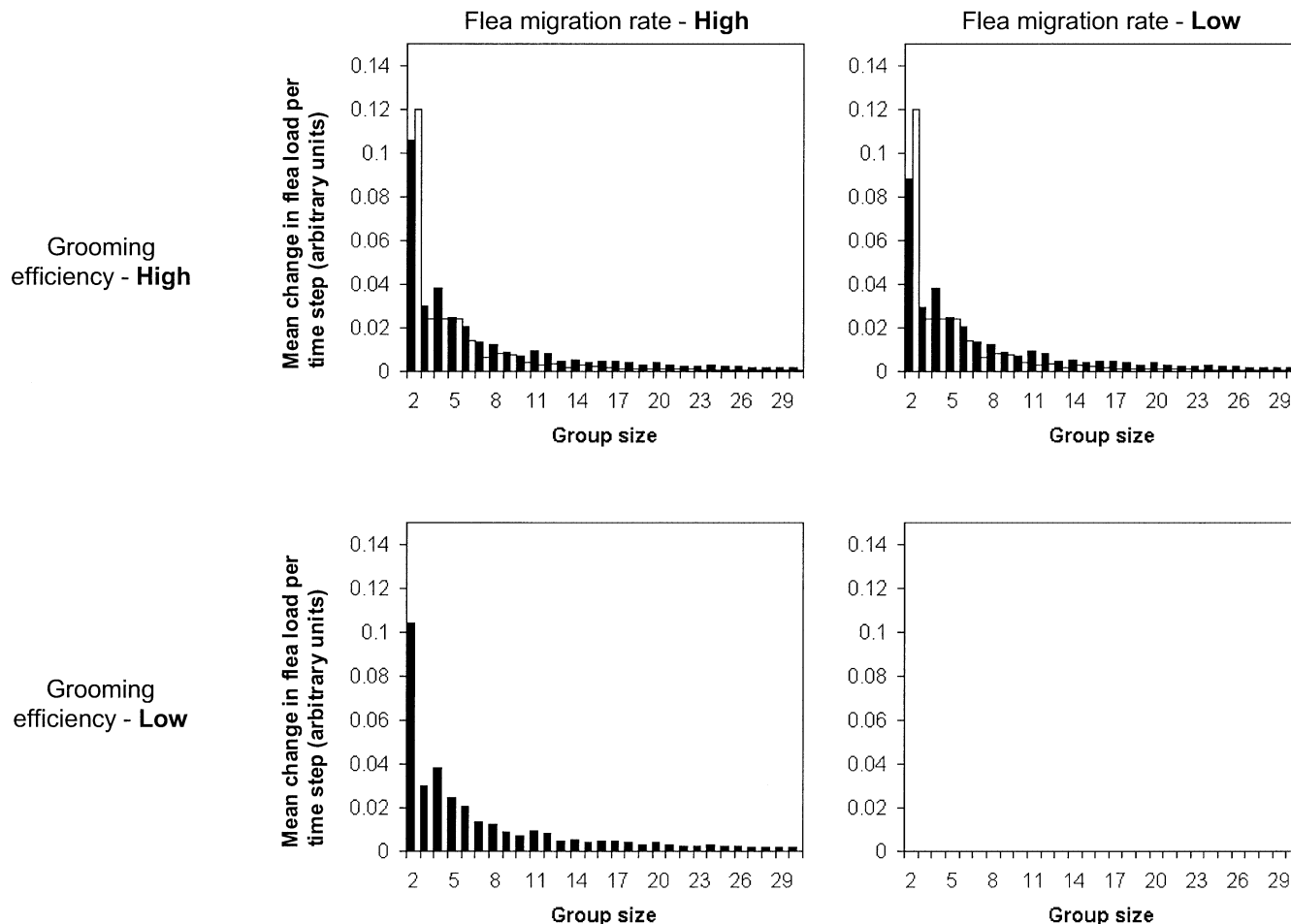


Figure 2

Simulated rates of change of mean flea burden (white bars) and flea burden variance (black bars) among group members for various group sizes. The two principal parameters responsible for these changes in flea burdens are (1) dilution due to flea migration and, (2) removal of fleas due to host allogrooming (with arbitrary high and low values for each). See “Model Results” section in main text for further interpretation of the four panels.

variance and mean per unit time; (2) variance in parasite loads should be greater between groups than within them (due to variance being suppressed within a group, regardless of the mean); (3) groups tend toward a discrete uniform distribution of flea burdens. Because we assume they start over each day, smaller groups, in which the dilution mechanism is more rapid, should exhibit these more flattened distributions of ectoparasites; (4) Groups nearer to each other are more likely to have similar flea burdens, assuming that the probability of intergroup contact declines with distance.

An empirical test

Methods

We had sufficient empirical data to test predictions 1 and 2. Field data come from European badgers, *M. meles* L. in Wytham Woods, 5 km Northwest of Oxford (01° 18' W, 51° 46' N), and their host specific flea, *Paraceras melis* (Macdonald and Newman, 2001). Allogrooming has been well documented at this site using infrared video (Macdonald et al., 2000; Stewart, 1997; Stewart et al., 1997) and is performed by all members of the social group (Cox et al., 1999; Stewart, 1997). Badgers spend a considerable amount of time involved in allogrooming at the sett (Macdonald et al., 2000; Stewart,

1997) and probably also below ground (Drabble, 1971). Allogrooming is not structured according to a dominance hierarchy (Macdonald et al., 2002b), nor is it exchanged for other benefits as has been demonstrated in primates (de Waal, 1997; Hemelrijk and Ek, 1991; Matheson and Bernstein, 2000; Parr, 1997) and mice (Stopka and Graciová, 2001; Stopka and Macdonald, 1999). When they groom, badgers draw hair between their teeth and apparently crush fleas once they are caught (Drabble, 1971; Neal and Cheeseman, 1996), which strongly suggests that grooming in badgers serves to remove fleas. *P. melis* could achieve IFD with relative ease as they jump between bodies of interacting hosts when the latter come into contact (Cox et al., 1999). Badgers become re-infested with fleas when they return to their underground setts during the daytime (Butler and Roper, 1996; Roper, 1992) and apparently change setts frequently to minimize this (Roper et al., 2001). Individuals of the same group need not have identical parasite loads simply as a result of emerging from the same setts, however, because they often utilize different regions within them, or indeed they may occupy different outlying setts within the group's territory (Roper et al., 2001).

We were able to collect data on individual badgers' flea burdens (trapped at their setts) four times every year, following identical methods since 1993. Flea loads were

Table 1
One-way ANOVAs to test whether variance in flea burdens is larger within or between badger groups

Year	df	<i>F</i>	<i>p</i>
Social groups			
1993	18,76	1.30	.211
1994	18,129	2.13	.008*
1995	19,206	4.88	<.0001*
1996	19,189	1.85	.020*
1997	20,162	1.32	.173
1998	19,160	2.39	.002*
Sett groups			
1993	21,73	1.41	.143
1994	23,124	1.66	.042*
1995	29,196	3.28	<.0001*
1996	29,179	1.62	.031*
1997	34,148	1.56	.037*
1998	34,145	2.48	.0001*

Variance was significantly greater among social groups than within them for 4 of the 6 years (1993–1998) and in 5 of the 6 years among sett groups. Significant relationships are flagged with asterisks. With Bonferroni-corrected significance levels for multiple comparisons, all four significant results among social groups remain significant, but the three weaker significant results among sett groups become nonsignificant. Bonferroni-corrected significance levels for multiple comparisons control for the increased number of type 1 error rates (false rejections of the null hypothesis) in a posteriori multiple significance testing (Rice, 1989). Standard Bonferroni tests are not adequate, because they increase type 2 error rates where more than one component hypothesis is false (i.e., they reduce power in detecting significant results). In this case, individual year tests were significant under the newly derived significance levels, judged by a test of $p_i \leq \alpha / (1 + k - i)$ where each *p* value is ranked in ascending order (p_1, p_2, \dots, p_i) for *k* tests (in this case *k* = 6, as six comparisons were made per variable and per social group category). The adjustment gives a different critical *p* value for each test.

estimated on immobile anesthetized badgers by taking a cumulative count while searching their fur for 20 s. This measure has been shown to be accurate and correlates significantly with longer counts ($p < .0001$), explaining 90% of the variance (Quinn, 2000). Throughout, we only analyzed data collected during the summers of each year (May–August) to control for seasonal variation. We tested predictions using two definitions of badger groups, either of which might represent more relevant cooperative units: (1) social groups, all residents from several different setts but which are known to share a communal territory; and (2) sett groups, residents of the same sett only.

RESULTS

Prediction 1 (group sizes should correlate with ectoparasite load)

Because parasite dilution occurs more rapidly in smaller groups (in which the model showed changes in flea variance and mean to be larger per unit time), group size is predicted to correlate positively with mean flea load and variance. We used a General Linear Model (GLM) to remove variance due to badger group identity while testing for associations between flea loads and group sizes. Social group size was correlated with flea load ($F_{21,96} = 1.753, p < 0.005$) and log flea variance ($F_{21,91} = 7.886, p = 0.006$), but not with raw flea variance ($F_{21,91} = 1.073, p = .303$; *p* values for the group identity variable in these three models were, respectively, $p = 0.038, p = .068$ and $p = .407$). The alternative category, sett group size, was not correlated with flea load ($F_{37,119} = 1.649, p = .202$),

or flea variance ($F_{34,106} = 0.027, p = .871$), or log flea variance ($F_{34,106} = 3.279, p = .073$; *p* values for the group identity variable in these three models were, respectively, $p = .015, p = .777$ and $p = .035$).

Prediction 2 (variance should be greater between social groups than within them)

One-way ANOVAs showed that in 4 of the 6 years, variance in flea loads was significantly greater between social groups than within them (unchanged with Bonferroni corrected significance levels for multiple comparisons), and this was true in 5 of the 6 years between sett groups (although only two remained so using Bonferroni corrected levels) (Table 1). *F* values were relatively high in the remaining cases that were judged as not significant.

The Bonferroni adjustment may be overly cautious because the variables under test are, to some extent, repeated each time—they are measures of things that are likely to be approximately similar in different years. Multiple inference tests are only problematic if tests are independent, not when multiple tests are likely to reject the null hypothesis for specific reasons. In the extreme scenario of our case, if group sizes and their associated flea loads remained relatively static over time while we measured them again each year, then regardless of the *p* value, after a certain number of years a Bonferroni adjustment will eventually become so small that no relationship can be significant. Our corrected results are therefore, if anything, conservative.

DISCUSSION

Empirical results were mixed. Predicted relationships should perhaps have been expected to be greater for sett group sizes rather than social group sizes, because members of the former category are apparently more likely to share the same setts and to meet more often. However, there is movement between the various outlying and main setts within the territories of social groups in this population (Macdonald and Newman, 2001; Stewart, 1997), so the differences between contact among these two groups is, at best, uncertain.

Alexander (1974) suggested that minimization of parasites was one of three principal factors leading to the evolution of social behavior among animals and humans. Despite this, theories of social grouping have tended to disregard the influence of parasites, even though there are good reasons to expect that they are significant. For instance, studies have shown that disease risk is related to group size (Brown and Brown, 1986; Hoogland, 1979; Poulin, 1991), social species are particularly prone to infection (Nunn et al., 2000), and grouping behavior can reduce infestation from biting flies by dilution (Mooring and Hart, 1992). Furthermore, many animals exhibit sophisticated behavioral and physical counter-ectoparasite adaptations (Connor, 1995). For example, “anting” behavior in birds and squirrels serves to control ectoparasites by allowing ants to swarm over them (Hauser, 1964), and primates use leaves, fruits and onion juice as insecticides on their fur (Freeland, 1976). The costs of parasite infestation are certainly not insignificant, and may be extremely high. In our study population of badgers, fleas carry potentially lethal parasites (Macdonald et al., 1999; Newman et al., 2001). The control of parasites is therefore likely to be an important selective pressure on social behavior. This may also be an important mechanism in understanding the interaction of social behavior and the spread of bovine tuberculosis, because suppurating wounds are thought to transfer the disease between badgers when they come into contact (Tuytens et al., 2000).

The notion that fleas tend to an IDF might be false if fleas bunch up on some individuals more than others. This could occur if low-ranking hosts are less able to allogroom, or if hosts in poor condition are better targets. However, in badgers there is no evidence of a social hierarchy or that allogrooming is related to any ranking structure among individuals (Macdonald et al., 2002b). Neither should hosts in poor health be more attractive to parasites. Rather, parasitizing ill individuals should be selected against (ill animals provide a suboptimal nutrient source, and if hosts are to die in isolation, resident ectoparasites may also be doomed).

Conclusions

The proposed dilution-grooming model presents a curious twist to the theory of IFD, whereby individual hosts can exploit the ideal-free migration of their mobile parasites to reduce their parasite burden—at least to the mean of the population—by mere contact with conspecifics. In such a system, there is also a consequent selective pressure to reduce this overall mean by allogrooming. When the group becomes large and the dilution mechanism slows down, the marginal advantages of being in the group decrease, so some individuals may then be better off leaving. This offers an explanation for the observation that groups fission when they become large in badgers (Da Silva et al., 1993; Newman, 2000) and other species (Baker et al., 2000; Dunbar, 1989; Macdonald, 1979). It also offers a functional basis for the apparent stability of badger social group sizes over time (Macdonald and Newman, 2001; Macdonald et al., 2002a).

This situation represents a public goods game (Kagel and Roth, 1995) in which everyone benefits by individual contributions, but one in which “free-riding” is of little benefit because badgers sleep in shared setts from which they can be re-infested each day (Roper, 1992; Roper et al., 2001). Any individual in contact with another risks being the destination of his opponent’s fleas, especially if that individual has a higher flea burden. Therefore, the cost of being parasitized is higher if allogrooming is not reciprocated, because some fraction of fleas will move anyway, even to a noncooperating individual. The best strategy is, therefore, to always reciprocate allogrooming, but to retaliate to a defection by the opponent with defection as well, such that all members of the population maintain an equal investment in allogrooming. This prediction is backed up by empirical evidence that allogrooming in badgers tends to be reciprocated with similar bout lengths (Macdonald et al., 2000; Stewart, 1997). At the extreme, if ectoparasites are shared more through communal sett use than through allogrooming, then it may simply be advantageous to groom everyone indiscriminately. In theory, at times when one has a relatively low flea burden, it could pay to defect from allogrooming to avoid others’ fleas. However, badgers frequently come into contact for numerous other reasons (mating, fighting, allomarking, etc.), so given the dilution effect and regular re-infestation from setts, it should remain in everyone’s interest to diminish the group mean. Thus, cheating may be precluded by the structure of the system.

After an initial spatial aggregation of individuals via mechanisms such as the resource dispersion hypothesis (Johnson et al., 2002; Macdonald, 1983), allogrooming could have evolved in a relatively simple step from parent-offspring grooming, to adult-adult grooming, as parents’ stakes in offspring transformed into reciprocal investment in other group members (which tend to be kin in badgers; Evans et al., 1989). Thus, the first step to sociality may be less dramatic than cooperative hunting or even alloparental care of

offspring, but instead may lie in the shared pursuit of parasites.

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