

# Cooperative Begging in Banded Mongoose Pups

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## Summary

Vivid begging displays are common in species with parental care [1, 2]. They are usually seen as the way that rival offspring selfishly compete over parental investment [3], and individuals are expected to respond to the begging of rivals by increasing their own begging intensity [4, 5]. Here I show the opposite—that potential rivals gain direct benefits from begging by littermates, so that begging behavior becomes a collective enterprise, similar to other cooperative activities. I investigate begging in communally breeding banded mongooses (*Mungos mungo*), where each pup forms an exclusive relationship with a single helper (its “escort”), minimizing competition over food allocation. Escorts were influenced by the total signal emanating from a litter, so that pups who begged at low rates received more food as litter size increased. Focal pups increased their begging when litters were experimentally reduced or littermates were induced to beg at low rates, but they received food at similar rates and showed reduced weight gain—indicating that they were paying a higher cost for a similar reward. These results suggest that offspring can benefit from companions despite conflicts over the allocation of parental investment [6, 7]. Such benefits provide an explanation for observed variation in the expression of parent-offspring conflict.

## Results

### Exclusivity of the Pup-Escort Association

Banded mongooses live in large family groups (average number of adults = 29, range 5–75) and are one of the few cooperative species where subordinates regularly breed (median breeding females = 4, range 1–12). Females give birth in synchrony, producing large communal litters (median litter size = 5, range 1–23), which remain in dens for 3–4 weeks. When pups emerge from the den, they spend 3–5 days approaching different helpers, after which individual pups form stable associations with a single adult helper (their “escort”) and remain associated with that animal until independence (approximately 9–13 weeks). Adults who do not become escorts thereafter provide very little pup care (see below). Escorts are generally young nonbreeding males

(1–3 yr old) or breeding females who contributed to the current litter. Associations are initiated and maintained by the pups [8], though the genetic relationship between escorts and pups remains unclear. During a foraging session, pups follow escorts closely (usually within 10 cm), begging constantly with a high-pitched, bird-like chirp (average call rate = 34.4 calls/min  $\pm$  0.73 standard error [SE], maximum = 80). Packs forage as a cohesive unit, concentrated within 15–20 m, so all escorts are exposed to begging by the whole litter (begging calls detected by an observer from 45 m, unpublished data).

Associations remain stable throughout the dependent period; pups receive their food almost exclusively from their escorts and are not in competition over the allocation of food items. Forty-eight percent of pups (30 of 63) associated with the same adult for every observation session and spent at least 40% of the time observed within 2 m of this adult (median = 94.4%, Interquartile Range [IQR] = 84.5%–100%). The remaining pups spent at least 70% of all observation sessions with the same adult (median = 94%, IQR = 84%–99%), though they spent at least one day associated with a different adult. Switches were always temporary, and only lasted for one day before pups returned to their original escort. No adult ever associated with more than one pup at the same time. Pups received a median of 100% of food items from their escorts (IQR = 86%–100%). In 73% of observation sessions, the focal pup received all of its food from its escort. No escort ever fed a pup associated with another adult.

### The Effect of Litter Size on Pup Begging Rate and Escort Provisioning Rate

Individual pups begged at significantly lower rates in larger litters (linear mixed model [LMM],  $\chi^2_{1,374} = 6.32$ ,  $p = 0.012$ ), after controlling for effects of time spent in association with an escort, pup age, pup condition, and escort age. Provisioning rate by individual escorts was influenced by an interaction between the begging rate of their associated pups and litter size, so that pups who begged at low rates received more food as litter size increased, whereas pups who begged at high rates always received food at high rates (LMM,  $\chi^2_{1,413} = 6.58$ ,  $p = 0.010$ ; Figure 1), after controlling for significant effects of time spent in association with an escort, escort age, and pup and escort sex.

### Manipulating Background Begging 1: Litter Reduction

When litter size was experimentally reduced by temporarily removing 1–2 pups, focal pups left in a pack significantly increased their begging rate (paired t test:  $n = 9$ ,  $t = 3.09$ ,  $p = 0.015$ ; Figure 2A) and the rate at which they were fed by their escorts significantly increased ( $n = 11$ ,  $t = 2.49$ ,  $p = 0.032$ ; Figure 2B), but they gained weight at a significantly lower rate ( $n = 11$ ,  $t = -2.42$ ,  $p = 0.036$ ; Figure 2C) (begging data for two pups were lost because of equipment failure).

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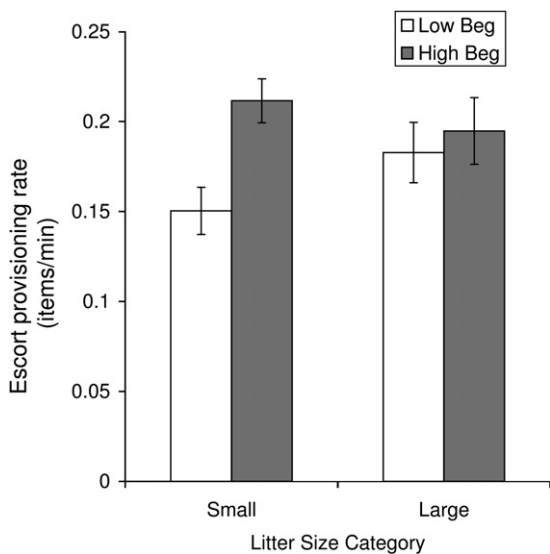


Figure 1. The Effect of Begging Rate and Litter Size on the Rate at which Escorts Feed Their Associated Pups

To illustrate the interaction, I converted both begging rate and litter size into 2-level factors by splitting the data at the median (begging rate: median = 35.8 begs per min; litter size: median = 4 pups). (Means  $\pm$  SE are shown.)

### Manipulating Background Begging 2: Reducing Littermate Begging while Keeping Litter Size Constant

When one or two littermates were induced to beg at lower rates by the temporary removal of their escorts, control pups still associating with their escorts significantly increased their begging rate (paired t test:  $n = 14$ ,  $t = 3.30$ ,  $p = 0.006$ ; Figure 2D), continued to be fed at the same rate ( $n = 14$ ,  $t = 0.55$ ,  $p = 0.591$ ; Figure 2E), and gained weight at a marginally lower rate ( $n = 14$ ,  $t = -2.13$ ,  $p = 0.053$ ; Figure 2F).

### The Effect of Litter Size on Changes in Begging after Deprivation

Experimentally deprived pups significantly increased begging rates. Those in large litters showed a lower percentage increase in begging than those in small litters, after controlling for significant effects of escort condition and pup sex (general linear regression,  $F_{1,19} = -8.18$ ,  $p = 0.01$ ; Figure 3).

### Discussion

Numerous studies have shown a variety of contradictory responses to begging by companions [5, 9, 10]. Recent theoretical [11] and empirical [12] studies suggest that this may be because offspring sometimes derive direct benefits from begging by companions—for instance, begging by host nestlings increases food delivery to brood parasites [12]. This is most likely to occur when carers are influenced by the total begging intensity of a brood [6, 13] and when competition between offspring over the allocation of resources is relaxed [11].

My results demonstrate that the unique pattern of cooperative care in banded mongooses minimizes competition between pups over the allocation of helper

investment, allowing pups to derive a clear benefit from begging by littermates. Focal pups begged at lower rates in larger litters, and those that begged at low rates received more food as litter size increased. In experimentally reduced litters, or when littermates were induced to beg at low rates, focal pups increased their begging rates and received similar amounts of food, yet gained weight at lower rates—indicating that they expended more energy for a similar reward when the background begging rate had been reduced. The escort system is therefore an excellent example of a situation where cooperative activity is favored after competition between individuals in a group has been restricted; such restrictions on individual competition have long been predicted to improve group efficiency and increase the average success of group members [14–16].

Numerous studies have investigated the effects of brood size on begging intensity (e.g., [17]), yet this is the first showing not only that focal offspring increase their begging rates after the background level of begging is experimentally lowered, but also that they incur a cost when they do so. This builds on studies that report similar responses to nestmate begging in barn owls [10] and black-headed gulls [18]. However, Roulin et al. [10] argued that the compensatory changes in begging they observed were due to negotiation between chicks to minimize the cost of competition, which is unlikely in banded mongooses for two reasons: first, because negotiation is predicted to occur in the absence of parents [19], and second, because the escort system effectively minimizes competition between pups over food allocation, and negotiation is only likely when there is direct competition between offspring. Mathevon and Charrier's [18] results are suggestive, but they do not account for differences in parental condition or provisioning ability, both of which may affect both brood size and chick begging.

As expected if pups can afford to invest less in begging as litter size increases, pup deprivation experiments demonstrated that experimentally deprived pups in larger litters showed a lower increase in begging than those in smaller litters. Numerous studies have demonstrated an increase in begging after deprivation (reviewed in [20, 21]). Few, however, have investigated what factors, other than degree of deprivation, influence the relative increase in begging after deprivation. This is the first study to find that deprived offspring increase their begging by less when the background signal is more intense.

Such adjustment of individual effort in relation to a collective output matches predictions made by models examining other forms of cooperative activity, where one individual is expected to reduce its own effort in response to an increase by others [22]. There are parallels with empirical results from many studies of cooperative activity, where individual contributions to a collective enterprise are reduced as the number of collaborators increases, e.g., babysitting [23], provisioning [24, 25], cooperative hunting [26], and vigilance [27, 28]. There is also evidence that individuals reduce their own effort when collaborators increase theirs [27, 29, 30]. It is often unclear, however, why such cooperative enterprises are not destabilized by free riders exploiting contributions

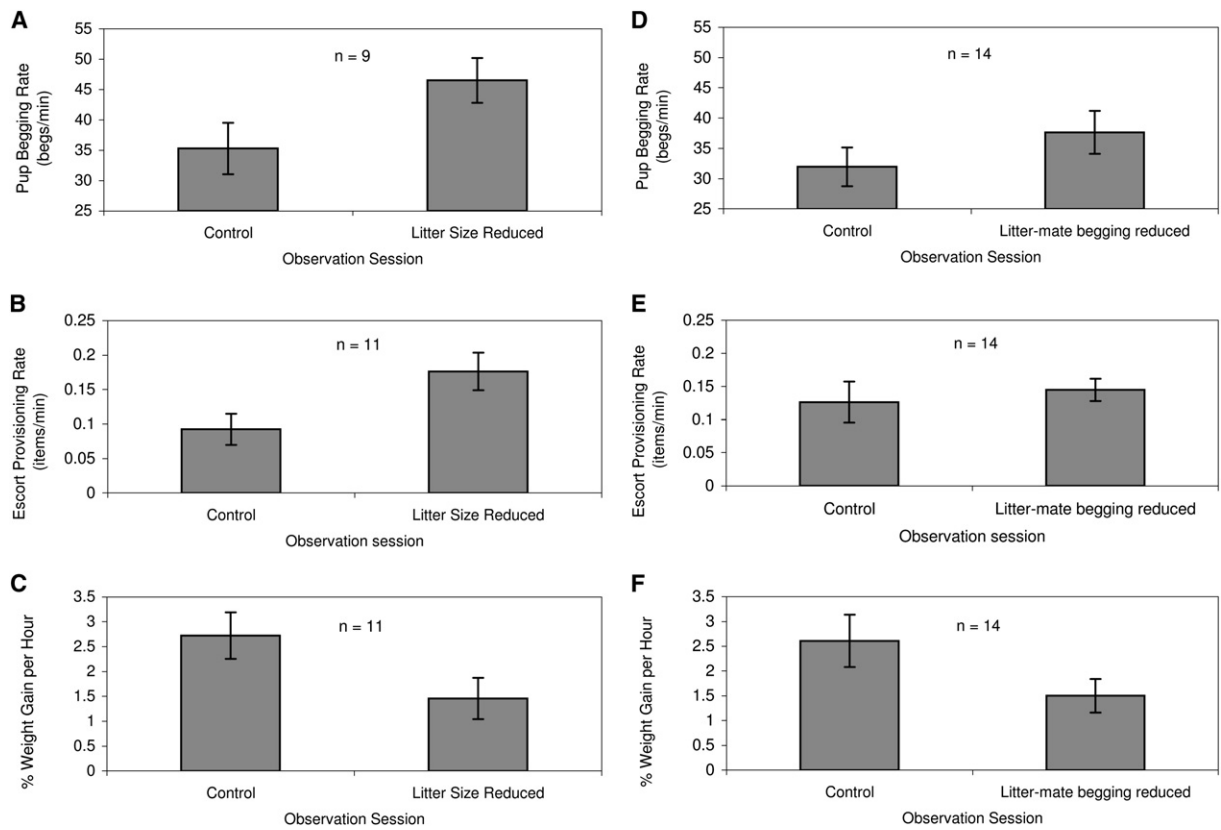


Figure 2. Experimentally Manipulating Background-Begging Intensity

The effect of reduced litter size on focal-pup begging rate (A), focal-escort provisioning rate (B), and focal-pup percentage hourly weight gain (C). The effect of reduced littermate begging rate on focal-pup begging (D), focal-escort provisioning rate (E), and focal-pup percentage hourly weight gain (F) is shown. (Means  $\pm$  SE are shown.)

by companions without contributing themselves. In banded mongooses, it is likely that hunger maintains individual contributions: A minimum level of begging may be required to stimulate feeding by escorts, and once the net signal from a litter drops below this level, all pups may suffer a shortfall. Recent models [31–33] have investigated the free-rider problem and propose similar solutions: The net productivity of groups “overburdened” by cheats declines to the extent where cheating becomes costly to the cheats themselves, so that the direct benefits to individuals of contributing to collective enterprises may be enough to stabilize cooperation.

Recent studies [34–36] go further and suggest that collaborators in a cooperative enterprise may even increase their own contribution to a cooperative activity in response to an increase by a collaborator. This may occur if individuals use collaborator effort as an indicator of the importance of increasing their own investment and may lead individuals to match changes in partner effort [35]. In a begging context, an increase in partner effort signals an increase in partner need, potentially informing broodmates that their indirect fitness is threatened by the starvation of a broodmate, or even that they run the risk of abandonment should brood size decline (e.g., [37]). Therefore, wherever carers are influenced by begging of whole broods, individuals may increase their own begging in order to increase

provisioning to needier broodmates. An escalation in response to an increase in begging by companions may not therefore be an indication of competition, but rather of an altruistic act. Whether or not this type of cooperative response occurs will depend on an individual’s own state, the way carers make decisions about the

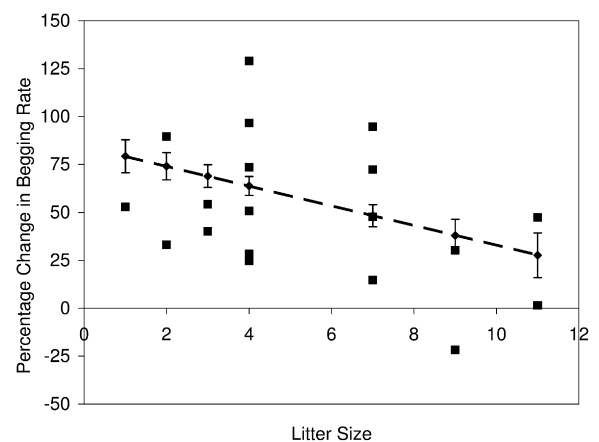


Figure 3. The Effect of Litter Size on the Percentage Change in Focal-Pup Begging Rate after Experimental Deprivation. Points are observed data, and line is predicted means from general linear regression  $\pm$  SE.

allocation of food, and the degree of competition between offspring. It does, however, potentially explain the mass of contradictory data regarding responses to broodmate begging.

The results presented here provide the first empirical evidence that offspring can gain a direct benefit from begging by companions, and suggest that a degree of cooperative begging may be more widespread, potentially offsetting underlying genetic conflicts. More generally, it seems likely that individuals stand to benefit from the combined output of a group in numerous signaling systems. Possible examples include floral displays attracting pollinators [38]; leks, or partnerships within leks, attracting females [39, 40]; conspicuous fruits attracting seed dispersers [41]; insect-nest parasites attracting hosts [42]; and Mullerian mimicry systems reinforcing the learned avoidance of aposematic patterns [43]. All have important shared properties: Each signaler incurs costs to participate; there are underlying genetic conflicts between the signalers; and the probability of a response, or the intensity of that response, increases with total signal intensity. Therefore, displays may not be as strictly selfish and competitive as previously thought, and it is important to consider the extent to which an individual display is concerned with contributing to a group effort to attract attention versus competing with groupmates over who benefits from that attention. Wherever competition between rival signalers is restricted, they should gain cooperative benefits from one another's signaling.

#### Experimental Procedures

Between May 2003 and August 2005, I observed 565 banded mongooses and monitored 68 successful breeding attempts from 13 packs in Queen Elizabeth National Park, Uganda (0°12' S; 27°54' E) (see [8] for habitat and climate details). Individuals are habituated to close (<5 m) observation on foot, and accurate ages ( $\pm 2$  days) are known for most of the population (92%). Individuals aged 0–3 months were classified as *pups* and >3 months as *helpers* (animals as young as 3 months have been observed provisioning pups, unpublished data).

For field identification, fully grown animals were fitted with color-coded plastic collars (weight 1.5 g). Growing animals and some well-habituated animals were given unique haircuts. Animals were trained to step on an electronic lab scale (accuracy  $\pm 1.5$  g) before foraging in the morning (approximately 07:30), and again after foraging in the evening (approximately 19:00). Individual condition was calculated as the residual from a linear regression of weight (g) over age (days). The percentage of hourly weight change was calculated as the total weight change (g) in a day, divided by morning weight, which was then divided by time (hr) between morning and evening weighing sessions. This research was carried out under license from Uganda National Council for Science and Technology, and all procedures were approved by the Uganda Wildlife Authority.

#### The Pup-Escort Relationship, Pup Begging, and Escort Feeding

To quantify associations between pups and helpers, I conducted 2 hr of scan observations each day once new litters started foraging. For each pup I recorded distance to ( $\pm 10$  cm) and identity of the nearest helper every 5 min. At the end of each session, I classified a helper as an escort if the same pup was within 2 m for  $\geq 40\%$  of scans. When pup habituation allowed, I conducted focal watches on pups by following each pup for  $\geq 20$  min, counting begging calls with a hand-held clicker, and recording ad libitum food items provided by helpers. At the end of every minute, I recorded the number of begging calls during that minute and the identity of every helper who was within 2 m of the pup for  $\geq 20$  s.

#### Experimental Data Collection

To investigate the effect of littermate begging on focal pups, I carried out two sets of experiments manipulating the background level of begging. In one set, I temporarily reduced litter size by removing one or two pups from a litter immediately after packs emerged in the morning, and then conducted focal watches on the remaining pups. In the other set, I temporarily removed the escorts of selected pups in a litter, which significantly reduces their begging rate. I then conducted focal watches on pups still in association with their escorts. Previous experiments had demonstrated that the disturbance caused by temporary (10 min) removal did not affect begging by either removed or control pups (see the [Supplemental Data](#) available online).

To investigate the effect of litter size on changes in begging rate in response to deprivation, I used the pups that had been removed during the litter-reduction experiments. During the removal (average duration 8.9 hr  $\pm 0.1$  SE) they were kept with ad lib water but no food, and I conducted focal watches on them when they were released.

#### Statistical Analysis

Where possible I carried out matched comparisons of individual behavior (all tests were two tailed). To investigate the variables influencing pup begging rates and escort provisioning rates, I used a general linear mixed model (LMM; see [Supplemental Data](#)). Means  $\pm$  SE are presented throughout.

#### Supplemental Data

Experimental Procedures and two tables are available at <http://www.current-biology.com/cgi/content/full/17/8/717/DC1/>.

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#### References

1. Kilner, R.M., and Johnstone, R. (1997). Begging the question: Are offspring solicitation behaviours signals of need? *Trends Ecol. Evol.* **12**, 11–15.
2. Wright J. and Leonard M.L., eds. (2002). *The Evolution of Begging: Competition, Cooperation and Communication* (Dordrecht, Netherlands: Kluwer).
3. Trivers, R.L. (1974). Parent-offspring conflict. *Am. Zool.* **14**, 249–264.
4. Godfray, H.C.J. (1995). Signalling of need between parents and young: Parent-offspring conflict and sibling rivalry. *Am. Nat.* **146**, 1–24.
5. Price, K., and Ydenberg, R. (1995). Begging and provisioning in broods of asynchronously hatched yellow-headed blackbird nestlings. *Behav. Ecol. Sociobiol.* **37**, 201–208.
6. Forbes, L.S. (1993). Avian brood reduction and parent-offspring "conflict". *Am. Nat.* **142**, 82–117.
7. Haig, D. (1996). Placental hormones, genomic imprinting, and maternal-fetal communication. *J. Evol. Biol.* **9**, 357–380.
8. Gilchrist, J.S. (2004). Pup escorting in the communal breeding banded mongoose: Behaviour, benefits and maintenance. *Behav. Ecol.* **15**, 952–960.
9. Kacelnik, A., Cotton, P.A., Stirling, L., and Wright, J. (1995). Food allocation among nestling starlings: Sibling competition and the

- scope of parental choice. *Proc. R. Soc. Lond. B. Biol. Sci.* 259, 259–263.
10. Roulin, A., Kolliker, M., and Richner, H. (2000). Barn owl (*Tyto alba*) siblings vocally negotiate resources. *Proc. R. Soc. Lond. B. Biol. Sci.* 267, 459–463.
  11. Johnstone, R.A. (2004). Begging and sibling competition: How should offspring respond to their rivals? *Am. Nat.* 163, 388–406.
  12. Kilner, R.M. (2003). How selfish is a cowbird nestling? *Anim. Behav.* 66, 569–576.
  13. Ottosson, U., Backmann, J., and Smith, H.G. (1997). Begging affects parental effort in the pied flycatcher, *Ficedula hypoleuca*. *Behav. Ecol. Sociobiol.* 41, 381–384.
  14. Leigh, E.G. (1977). How does selection reconcile individual advantage with the good of the group? *Proc. Natl. Acad. Sci. USA* 74, 4542–4546.
  15. Alexander, R.D. (1979). *Darwinism and Human Affairs* (Seattle: University of Washington Press).
  16. Frank, S.A. (2003). Repression of competition and the evolution of cooperation. *Evolution Int. J. Org. Evolution* 57, 693–705.
  17. Leonard, M.L., Horn, A.G., Gozna, A., and Ramen, S. (2000). Brood size and begging intensity in nestling birds. *Behav. Ecol.* 11, 196–201.
  18. Mathevon, N., and Charrier, I. (2004). Parent-offspring conflict and the coordination of siblings in gulls. *Proc. Biol. Sci.* 271, S145–S147.
  19. Johnstone, R.A., and Roulin, A. (2003). Sibling negotiation. *Behav. Ecol.* 14, 780–786.
  20. Royle, N.J., Hartley, I.R., and Parker, G.A. (2002). Begging for control: When are offspring solicitation behaviours honest? *Trends Ecol. Evol.* 17, 434–440.
  21. Leonard, M.L., and Horn, A.G. (1998). Need and nest-mates affect begging in tree swallows. *Behav. Ecol. Sociobiol.* 42, 431–436.
  22. McNamara, J.M., Gasson, C.E., and Houston, A.I. (1999). Incorporating rules for responding into evolutionary games. *Nature* 401, 368–371.
  23. Clutton-Brock, T.H., Gaynor, D., Kansky, R., MacColl, A.D.C., McIlrath, G.M., Chadwick, P., Brotherton, P.N.M., O’Riain, J.M., Manser, M., and Skinner, J.D. (1998). Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proc. R. Soc. Lond. B. Biol. Sci.* 265, 185–190.
  24. Clutton-Brock, T.H., Brotherton, P.N.M., O’Riain, M.J., Griffin, A.S., Gaynor, D., Kansky, R., Sharpe, L., and McIlrath, G.M. (2001). Contributions to cooperative rearing in meerkats. *Anim. Behav.* 61, 705–710.
  25. MacColl, A.D.C., and Hatchwell, B.J. (2003). Sharing of caring: Nestling provisioning behaviour of long-tailed tit, *Aegithalca caudatus*, parents and helpers. *Anim. Behav.* 66, 955–964.
  26. Creel, S., and Creel, N.M. (2002). *The African Wild Dog: Behaviour, Ecology and Conservation* (Princeton and Oxford: Princeton University Press).
  27. Clutton-Brock, T.H., O’Riain, M.J., Brotherton, P.N.M., Gaynor, D., Kansky, R., Griffin, A.S., and Manser, M. (1999). Selfish sentinels in cooperative mammals. *Science* 284, 1640–1644.
  28. Wright, J., Berg, E., de Kort, S.R., Khazin, V., and Maklakov, A.A. (2001a). Safe, selfish sentinels in a cooperative bird. *J. Anim. Ecol.* 70, 1070–1079.
  29. Wright, J., Maklakov, A.A., and Khazin, V. (2001b). State-dependent sentinels: An experimental study in the Arabian babbler. *Proc. R. Soc. Lond. B. Biol. Sci.* 268, 821–826.
  30. Wright, J., and Dingemanse, N.J. (1999). Parents and helpers compensate for experimental changes in the provisioning effort of others in the Arabian babbler. *Anim. Behav.* 58, 345–350.
  31. Kokko, H., Johnstone, R.A., and Clutton-Brock, T.H. (2001). The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. Lond. B. Biol. Sci.* 268, 187–196.
  32. Aviles, L. (2002). Solving the freeloader paradox: Genetic associations and frequency-dependent selection in the evolution of cooperation among non-relatives. *Proc. Natl. Acad. Sci. USA* 99, 14268–14273.
  33. Hauert, C., Holmes, M., and Doebeli, M. (2006). Evolutionary games and population dynamics: Maintenance of cooperation in public goods games. *Proc. R. Soc. Lond. B. Biol. Sci.* 273, 2565–2570.
  34. Hinde, C.A. (2006). Negotiation over offspring care? – a positive response to partner provisioning rate in great tits. *Behav. Ecol.* 17, 6–12.
  35. Johnstone, R., and Hinde, C.A. (2006). Negotiation over offspring care – how should parents respond to each others efforts? *Behav. Ecol.* 17, 818–827.
  36. Valencia, J., de la Cruz, C., Carranza, J., and Mateos, C. (2006). Parents increase their parental effort when aided by helpers in a cooperatively breeding bird. *Anim. Behav.* 71, 1021–1028.
  37. Eadie, J.M., and Lyon, B.E. (1998). Cooperation, conflict, and creching behavior in goldeneye ducks. *Am. Nat.* 151, 397–408.
  38. Ghazoul, J. (2005). Pollen and seed dispersal among dispersed plants. *Biol. Rev. Camb. Philos. Soc.* 80, 413–443.
  39. Widemo, F., and Owens, I.P.F. (1995). Lek size, mating skew and the evolution of lekking. *Nature* 373, 148–151.
  40. Krakauer, A.H. (2005). Kin selection and cooperative courtship in wild turkeys. *Nature* 434, 69–72.
  41. Burns, K.C. (2005). Does mimicry occur between fleshy fruits? *Evol. Ecol. Res.* 7, 1067–1076.
  42. Saul-Gershenz, L.S., and Millar, J.G. (2006). Phoretic nest parasites use sexual deception to obtain transport to their host’s nest. *Proc. Natl. Acad. Sci. USA* 103, 14039–14044.
  43. Alatalo, R.V., and Mappes, J. (1996). Tracking the evolution of warning signals. *Nature* 382, 708–710.