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Facultative response to a kleptoparasite by the cooperatively breeding pied babbler

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In many cases of interspecific kleptoparasitism, hosts develop defensive behaviors to minimize the impact of kleptoparasites. Because vigilance and defensive behaviors are often costly, selection should favor hosts that adjust the amount of investment needed to minimize losses to kleptoparasitism. However, examples of such facultative responses are rare. Here, we investigate the response of cooperatively breeding pied babblers (*Turdoides bicolor*) to the drongo (*Dicrurus adsimilis*), an avian kleptoparasite that regularly follows pied babbler groups, often giving alarm calls to alert the group to predators but also occasionally giving false alarm calls in order to steal food items. We show that pied babbler response to drongos varies markedly according to babbler group size. In small groups, where there are few individuals available to act as sentinels, babblers sentinel less when a drongo is present and respond strongly to drongo alarm calls. However, in large groups, where there are many individuals available to participate in predator vigilance, babblers sentinel more often when a drongo is present, rarely respond to drongo alarm calls, and aggressively displace drongos, with a consequent decline in the number of successful kleptoparasitism events. This behavior represent a facultative response to a kleptoparasite according to the costs versus benefits of tolerating their presence. *Key words:* cooperative breeding, drongo, facultative response, kleptoparasitism, pied babbler, sentinel behavior, *Turdoides bicolor*. *[Behav Ecol 18:324–330 (2007)]*

Interspecific kleptoparasitism is a well-known foraging tactic occurring across a wide range of bird species (for reviews, see Brockmann and Barnard 1979; Furness 1987). In many cases, hosts adopt defensive behaviors to avoid or minimize kleptoparasitism (Brockmann and Barnard 1979; Cangialosi 1990). Such defensive behaviors may inflict energetic costs on hosts such as lost foraging time, lower food intake rate, and higher levels of vigilance (Lima 1991; Beauchamp 1998; Giraldeau and Caraco 2000; Morissette and Himmelman 2000; Fritz et al. 2002). Thus, host response to kleptoparasites may be expected to vary according to the intensity of kleptoparasitism (Stillman et al. 1997), allowing hosts to facultatively adjust the amount of energy invested in defense according to the costs versus benefits of such behavior. However, examples of such facultative responses by host species are rare.

Cooperatively breeding species, where group members commonly cooperate to defend resources, may provide one of the best opportunities to observe facultative responses to kleptoparasites because the number of individuals present in a group may affect the group's ability to invest in defense against kleptoparasites. In large groups, where there are many group members to share the cost of vigilance and defensive behaviors (Quenette 1990), individuals may invest more time actively displacing kleptoparasites, thereby minimizing the number of successful kleptoparasitism events. As the number of group members available to participate in defense and vigilance changes, the response to kleptoparasites may also change. In wild dogs (*Lycaon pictus*), for example, large groups are less likely to have prey kleptoparasitized by lions (*Panthera leo*) and hyenas (*Crocuta crocuta*) because there are sufficient group members to effectively defend the catch, whereas small groups are more likely to relinquish a catch to escape the threat of injury (Carbone et al. 1997, 2005; Courchamp et al. 2002). Thus in small groups, the cost of repelling kleptoparasites may be high and group members may consequently be more likely to tolerate kleptoparasitism events and even use the presence of a kleptoparasite to their advantage (e.g., for added predator vigilance).

In this paper, we investigate the effect of group size on the response of the cooperatively breeding pied babbler (*Turdoides bicolor*) to the presence of the fork-tailed drongo (*Dicrurus adsimilis*), a medium-sized passerine that perches above and follows foraging babbler groups. When following babbler groups, drongos give alarm calls to alert the group to the presence of predators but also occasionally give false alarm calls to displace babblers and kleptoparasitize food items. Pied babbler groups allocate a high proportion of time to vigilance behavior, resulting in a loss in the amount of time available to forage and provision young (Ridley AR, unpublished data). To achieve similar predator vigilance rates to large groups, members of small groups must individually allocate a higher proportion of time to predator vigilance, resulting in a considerable loss of foraging time. Babblers in small groups should therefore tolerate the presence of drongos if they provide additional predator vigilance. However, in large groups with sufficient members to provide high levels of predator vigilance, the benefit to tolerating drongos may be less, and large groups should therefore be more likely to aggressively displace drongos from the foraging area to minimize kleptoparasitism events. Our analysis examines the effect of group size on babbler sentinel behavior, the intensity of response to drongo alarm calls, and aggression rates toward drongos. We also investigate whether group size affects the number of successful kleptoparasitism events for drongos and discuss the implications of changes in group size for babbler–drongo interactions.

METHODS

Study site and population

We studied interactions between babblers and drongos in 21 groups of pied babblers at the Kuruman River Reserve in the southern Kalahari Desert, South Africa (26°58′S, 21°49′E) between October 2003 and March 2004. The study area is

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semi-arid grassland and acacia savanna, with an average annual rainfall of 217 mm (a detailed description of the climate and vegetation is given in Clutton-Brock et al. 1999).

Pied babblers are medium-sized passerines (75–95 g) occupying the semi-arid regions of southern Africa. Groups defend year-round territories and forage closely together throughout the day. Pied babblers are relatively terrestrial, with more than 95% of foraging time spent on the ground. Individuals use their bills to dig in the substrate for prey, and as a consequence they cannot forage and remain vigilant for predators simultaneously. Foraging babblers therefore rely on alarm calls from sentinels to alert them to the presence of predators, with 68.8% (±3.6) of all alarm calls given by a sentinel. All adult group members (individuals greater than 12 months old) participate in sentinel behavior.

Babbler group size during the study period ranged between 2 and 12 individuals, averaging 4.6 ± 0.8 adults per group. All pied babblers at the study site were individually recognizable using a unique combination of colored rings, and both babblers and drongos were habituated to observation from a distance of approximately 2–3 m. Prior to data collection, each group was habituated to the presence of an observer for several weeks. Each group was visited daily during the habituation process, and a group was considered habituated when they continued normal foraging behavior and neither gave alarm calls, flew to cover, or became vigilant when an observer approached. The time spent in habituation was equal across all groups included in the study.

Drongos (45–65 g) are solitary foragers that occasionally invest in interspecific kleptoparasitic behavior, stealing food items from many small to medium-sized bird species and several small mammal species (Hockey et al. 2005). Individual drongos often follow babbler groups, perching above the group and moving between foraging sites with them. While drongos are following babbler groups, they commonly do not forage for themselves, but upon capture of a large prey item by a babbler, the drongo may give an alarm call to frighten the foraging individual and subsequently attempt to steal the dropped food item. Drongos also regularly give reliable alarm calls upon sighting a predator and have been observed to mob or physically attack predators approaching babbler groups. Drongos were observed at babbler groups for an average of 12.2% (±2.1) of observation time. A drongo was considered to be present at a babbler group when it was less than 5 m away from the most peripheral babbler and actively following the group between foraging areas.

Data collection

Each babbler group was observed for a minimum of 3 h every 5 days (starting at dawn when the group left the roost tree), during which the duration of all sentinel behavior by both babblers and drongos was recorded. Sentinel behavior was defined as an adult perched in an elevated position (greater than 1 m from the ground) above the foraging group and actively scanning the horizon. Sentinel bouts were recorded on handheld data loggers and timed to the nearest minute. During each observation session, all adult predator alarms (from both babblers and drongos) were recorded, and the response of the foraging group was recorded as "strong," "weak," or "no response." A response was considered strong if the group mobbed the predator in question, alarmed and took flight, or immediately fled to cover. A weak response was if the group simply became alert and scanned the area for predators or moved closer to cover, and no response was where the alarm call had no discernible effect on the foraging behavior of the group. A response was only recorded if at least 50% of the adult group members responded.

It is possible that different categories of predator cause a different level of response based on perceived risk and distance from the group (Cheney and Seyfarth 1990; Leavesley and Magrath 2005). To avoid this potential problem, the analysis was confined to predators that were less than 100 m from the group at the time of alarm. These predators included all raptors greater than 300 g normally resident at the reserve (including pale chanting goshawk, *Melierax canorus* and lanner falcon, *Falco biarmicus*), yellow mongoose (*Cynictis penicillata*), slender mongoose (*Galerella sanguinea*), small spotted genet (*Genetta genetta*), African wild cat (*Felis silverstris*), puff adder (*Bitis arietans*), and Cape cobra (*Naja nivea*).

All incidences of aggression between babblers and drongos were recorded. Aggression was defined as one individual charging at and displacing another or one individual physically attacking another. A kleptoparasitism attempt was considered to have occurred when a drongo gave an alarm call without any predator apparent and immediately swooped down upon a babbler carrying a food item.

Analysis

All results presented are based on 1421.8 h of observation, during which babblers invested 343.5 h and drongos 91.9 h in sentinel activity. We checked that the data met all the assumptions of the statistical tests used and transformed data where necessary. Data were analyzed using normally distributed GLMMs (general linear mixed models) in Genstat 8.1 (Genstat 8th Edition, Lawes Agricultural Trust, 2005), which allow repeated measures to be fitted as random terms, thus controlling for their effects on the distribution of the data. The method of fitting GLMMs to data followed Crawley (2002). Model simplification using backward elimination was adopted. Terms were systematically removed from the model and only put back in if their removal resulted in a significant loss of model explanatory power. All biologically plausible interactions were included in the saturated model, but only significant interactions are presented. This technique of model fitting was adopted for all analyses. Throughout the text, means are expressed with standard errors, and null hypotheses are rejected at $P < 0.05$.

The effect of group size on sentinel behavior

To determine whether members of small groups spent more time as sentinels than members of large groups, we investigated the relationship between group size (number of adult members) and the proportion of total observation time involved in sentinel behavior per babbler. Group identity was included as a random term in the model. We then investigated the effect of drongos on babbler sentinel behavior by calculating the proportion of observation time spent as sentinel when a drongo was present at the group, with that when a drongo was absent, for all individuals. The effect of drongo presence was analyzed by assigning the number "0" to sentinel activity when a drongo was absent and the number "1" to sentinel activity when a drongo was present. This was entered as a categorical predictor into a GLMM where the response variable was the proportion of observation time involved in sentinel activity per individual. Group and individual identities were included as random terms in the model.

To determine whether sentinel behavior changed after a change in group size and whether drongo presence affected this behavior, we investigated the amount of time that each individual spent as sentinel in the presence of a drongo before and after the loss of a group member (through either dispersal or predation). Data were restricted to those groups that lost only one group member during the study period

($n = 6$ groups). For each individual, the proportion of total observation time spent as sentinel in the month before and after the loss of a group member was entered as the response variate in a GLMM. The effect of group member loss on sentinel behavior was investigated by assigning the number 0 to sentinel activity in the month prior the loss and the number 1 to sentinel activity in the month after. Group size was added as a covariate in the model. Group and individual identities were included as random terms. An additional GLMM using the same potential explanatory terms was conducted with the response variable changed to the proportion of observation time spent guarding when a drongo was not present.

The effect of group size on babbler response to drongos

The effect of group size on babbler response to drongo alarm calls was investigated using the percentage of all true drongo alarm calls ($n = 291$) to which babblers gave "no response" or a "strong response" for each group. A "true" alarm call was defined as an alarm call given when a predator was visible. To ensure the results were a consequence of group size and not extrinsic factors, we included the percentage of babbler alarm calls to which the group gave "no response" or a "strong response" over the same time period as a covariate. Group identity was included as a random term in the model.

The effect of group size on the frequency of aggression from babblers toward drongos was analyzed using the number of times that each individual babbler ($n = 120$) was observed aggressively chasing or displacing a drongo. The total number of aggressive acts by each babbler was divided by the total number of hours that a drongo was present at the focal babbler's group to give an average value of the number of aggressive attacks per hour of drongo presence. This was used as the response variable in a normally distributed GLMM with an identity link function. Group size was entered as a potential explanatory term, and group identity was included as a random term in the model. Drongo aggression rates toward babblers were not analyzed because such aggression was rare and primarily directed toward juveniles.

The cost of responding to drongos

We investigated the relationship between group size and the rate of successful kleptoparasitism for drongos by calculating the number of false alarm calls given by drongos that resulted in successful kleptoparasitism per hour that drongos spent as sentinels above each babbler group. The number of attempted kleptoparasitisms was included as a covariate in the model to control for the possibility that the number of successful kleptoparasitisms was a consequence of the number of attempts rather than an effect of babbler group size. Group identity was included as a random term in the model.

RESULTS

The effect of group size on sentinel behavior

When foraging in the absence of drongos, babblers in small groups spent more time (per individual) as sentinels than babblers in large groups (GLMM: $\chi^2 = 13.99$, $P < 0.001$, $n = 120$ babblers, Figure 1), resulting in no difference in the proportion of total observation time that a sentinel was present between groups of different sizes (linear regression: $F_{1,20} = 0.93$, $P = 0.35$). The effect of drongo presence on babbler sentinel behavior varied according to group size (Figure 2). In small groups, individuals spent less time as sentinels when a drongo was present than when a drongo was absent,

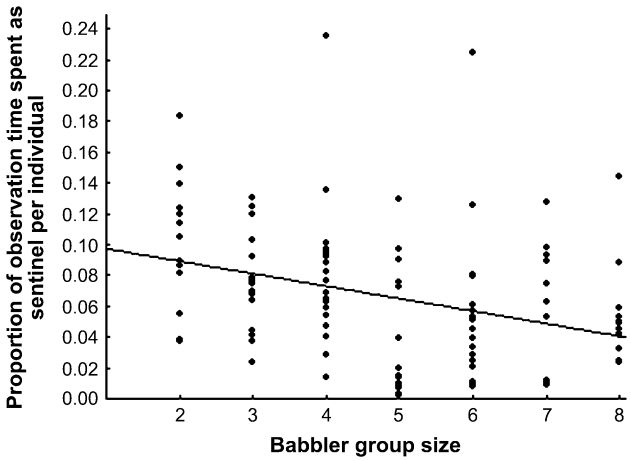

Figure 1
The proportion of observation time spent as sentinel per individual babbler when a drongo was absent in relation to babbler group size. Raw data values are displayed. The line of best fit is generated from GLMM predictions.

whereas individuals in large groups tended to sentinel more often when a drongo was present (Table 1). The amount of sentinel time saved per individual in small groups when a drongo was present was therefore substantial, with each individual saving an average of 11.9% (±1.7) of observation time normally spent as sentinel.

The effect of drongo presence on sentinel behavior was emphasized in groups that changed size during the study period. In several groups that lost a group member though dispersal or predation, there was no difference in the proportion of total observation time that a sentinel was present when a drongo was absent compared with preloss levels (paired t-test: $t = -1.48$, $P = 0.19$, $n = 6$), suggesting remaining group members increased their sentinel time to compensate for the loss (mean proportion of time spent as sentinel per individual before loss: 0.071 ± 0.002, after loss: 0.084 ± 0.010, Table 2 [Drongo absent]). In contrast, when a drongo was present, remaining group members spent less time guarding

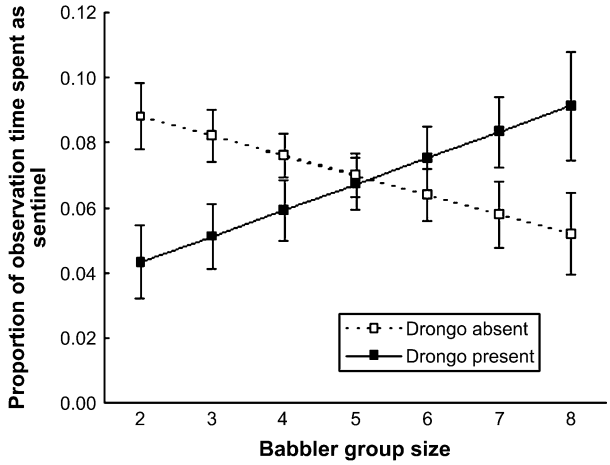

Figure 2
The proportion of observation time that individuals spent as sentinels when a drongo was absent compared with when a drongo was present in relation to babbler group size. The means and standard errors are generated from the predictions of the GLMM presented in Table 1.

Table 1
GLMM analysis of the terms associated with the proportion of observation time spent as sentinel per individual

Model term	Wald statistic	df	*P*
Full model			
Drongo presence × group size	33.37	1	<0.001
Drongo presence	4.85	1	0.028
Group size	1.01	1	0.314
	Average effect	SE	
Minimal model			
Constant	0.064	0.007	
Drongo presence	−0.012	0.005	
Drongo presence × group size	−0.017	0.004	

Analysis was conducted on 120 individuals from 21 different groups. Group identity was included as a random term in the model. df, degrees of freedom; SE, standard error.

compared with preloss levels (mean proportion of time spent as sentinel per individual before loss: 0.064 ± 0.007, after loss: 0.050 ± 0.008, Table 2 [Drongo present]), thereby minimizing the extra effort required to maintain predator vigilance at the same level as prior the loss.

The effect of group size on babbler response to drongos

The proportion of drongo alarm calls to which babblers gave a strong response declined as group size increased (Table 3, Figure 3a), whereas the proportion of drongo alarms to which babblers failed to respond increased (Table 4, Figure 3b). It is unlikely that this effect is influenced by a difference in responsiveness to all alarm calls with increasing group size, as there was no relationship between group responsiveness to babbler alarm calls and drongo alarm calls over the same time period (Tables 3 and 4).

The benefit to babblers of having drongos present for predator detection was lowest in large groups where there were many individuals available to share sentinel duty, and consequently aggression toward drongos was most common in large groups (GLMM: $\chi^2 = 28.70$, $P < 0.001$, $n = 120$ babblers in 21 different groups). In large groups, babblers were observed actively displacing drongos from the foraging area, decreasing the chance of drongos successfully stealing food items. Aggression toward drongos was rarely observed in small groups (Figure 4).

Table 3
GLMM analysis of the terms associated with the proportion of total drongo alarm calls given at each babbler group to which the group gave a strong response

Model term	Wald statistic	df	*P*
Full model			
Group size	10.99	1	<0.001
Proportion of babbler alarms to which group gave a strong response	0.51	1	0.474
	Average effect	SE	
Minimal model			
Constant	0.105	0.056	
Group size	−0.092	0.027	

Analysis was conducted on 21 different groups. Group identity was included as a random term in the model. df, degrees of freedom; SE, standard error.

The cost of responding to drongos

In small groups, where babblers responded strongly to drongo alarm calls and were rarely aggressive, drongos were more likely to successfully kleptoparasitize food items (Table 5), despite no difference in the frequency of false alarm calls given by drongos between groups of different sizes (Linear regression: $F_{1,20} = 1.33$, $P = 0.264$). The average rate of successful kleptoparasitism for drongos when following small babbler groups was 1.17 steals per hour compared with 0.16 steals per hour at large babbler groups (Figure 5).

DISCUSSION

Pied babblers exhibit wide variation in behavioral response to the kleptoparasitic drongo, with this variation strongly dependent on the number of group members available to participate in predator vigilance. Such facultative response to drongo presence allows pied babblers to minimize the impact of kleptoparasitism in large groups and maximize the benefit received from an extra vigilant individual in small groups.

Small groups need to maintain a level of predator vigilance comparable with larger groups to avoid predation, but with fewer members the high amount of time spent vigilant per individual may constrain food intake rate (Beauchamp 1998; Lima et al. 1999; Giraldeau and Caraco 2000). Members of small groups may therefore achieve a considerable time saving

Table 2
GLMM analysis of the terms associated with the mean proportion of observation time spent as sentinel per individual when (a) a drongo was absent and (b) a drongo was present 1 month before and after the loss of a single group member

	Drongo absent			Drongo present		
Model term	Wald statistic	df	*P*	Wald statistic	df	*P*
Full model						
Loss of group member	2.86	1	0.091	4.21	1	0.040
Group size	1.75	1	0.186	0.01	1	0.963
	Average effect	SE		Average effect	SE	
Minimal model						
Constant	0.063	0.01		0.052	0.07	
Loss of group member				−0.02	0.01	

Analysis was conducted on 56 monthly sentinel rates from 28 individuals in 6 different groups. Group and individual identity were included as random terms in each model. df, degrees of freedom; SE, standard error.

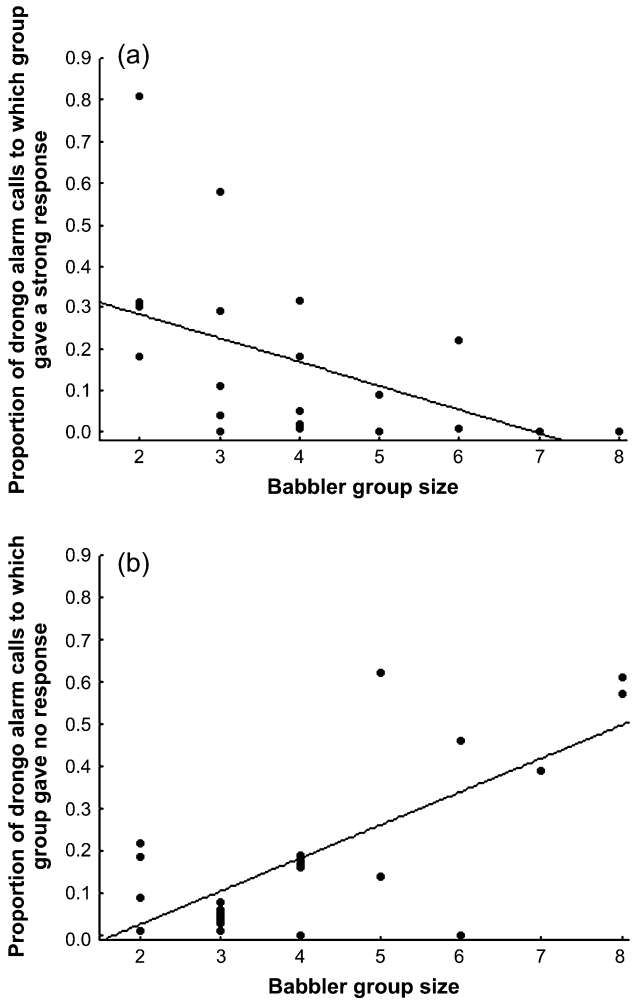

Figure 3
The proportion of true drongo alarm calls to which babbler groups gave (a) a strong response and (b) no response in relation to babbler group size. The lines of best fit are generated from the predictions of the GLMMs presented in Tables 3 and 4.

Table 4
GLMM analysis of the terms associated with the proportion of total drongo alarm calls given at each babbler group to which the group gave no response

Model term	Wald statistic	df	*P*
Full model			
Group size	7.51	1	0.006
Proportion of babbler alarms to which group gave no response	0.22	1	0.635
	Average effect	SE	
Minimal model			
Constant	0.202	0.042	
Group size	0.079	0.029	

Analysis was conducted on 21 different groups. Group identity was included as a random term in the model. df, degrees of freedom; SE, standard error.

by cueing in on alarm calls given by drongos rather than having a babbler sentinel present for predator detection. The time saved may then be invested in other cooperative activities such as provisioning young, potentially reducing the negative effect of limited helper number on offspring growth and development (e.g., Emlen and Wrege 1991; Mumme 1992; Russell et al. 2002; Hodge 2005), or maintaining body condition. Such time savings suggest drongo sentinels could effectively "lighten the load" (Crick 1992) for members of small groups.

The potential load-lightening benefit of using drongos as extra predator vigilance is evident after the loss of a group member. After a loss, remaining individuals tended to rely more on drongos for predator vigilance, minimizing the extra effort required from remaining group members to maintain predator vigilance at the same level as prior the loss. The potential benefit to small groups of extra vigilance from drongo presence was emphasized by the predation rate during the study period. Although incidences of observed predation were very low ($n = 6$), all occurred in small groups and all occurred when a drongo was absent. We suggest that, because of the probable increased vulnerability to predators in small groups (Lima et al. 1999; reviewed in Elgar 1989), pied babblers resident in small groups benefit most from accepting a low level of kleptoparasitism and actually achieve some benefit from drongo vigilance. In large groups, where additional group members may negate the vigilance benefit received from tolerating drongos, babblers do best by not responding to drongo alarm calls and by actively displacing drongos from the area, thereby minimizing the number of losses to kleptoparasitism, similar to the group size effect observed in wild dog–lion and hyena interactions (Carbone et al. 1997, 2005; Courchamp et al. 2002).

There has been considerable debate surrounding the ability of species to facultatively respond to changing conditions (Rothstein 1990; Ball and Baker 1996; Broom and Ruxton 1998; Juliano and Gravel 2002), with some authors suggesting that species are only able to give a fixed response to current conditions, with adaptive changes occurring relatively slowly over evolutionary time (Rothstein 1990; Shealer et al. 2005). Our results agree with those of Juliano and Gravel (2002) and Eggers et al. (2005) that facultative adjustment of behavior can occur extremely quickly in response to change. This flexibility allows species to quickly adapt, thereby minimizing

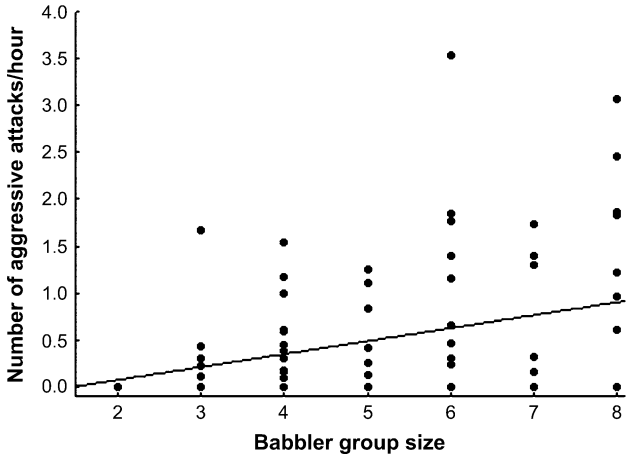

Figure 4
The number of times that each babbler was observed aggressively chasing or displacing a drongo per hour that a drongo was present at the group in relation to babbler group size. The line of best fit is generated from GLMM predictions.

Table 5
GLMM analysis of the terms associated with the number of successful kleptoparasitisms at each group per hour by drongos

Model term	Wald statistic	df	*P*
Full model			
Group size	15.13	1	<0.001
Number of kleptoparasitism attempts	3.04	1	0.095
	Average effect	SE	
Minimal model			
Constant	−1.006	0.206	
Group size	−0.510	0.131	

Analysis was conducted on 159 instances of attempted kleptoparasitism in 21 different babbler groups. Group identity was included as a random term in the model. df, degrees of freedom; SE, standard error.

the potential negative effects suffered from a change in conditions.

Recent theoretical models have modeled kleptoparasitism as a context-dependent foraging strategy that depends on food availability, the distribution of potential hosts, and the ease at which food can be stolen (Broom and Ruxton 1998, 2003; Hamilton 2002). The lack of variation in the number of kleptoparasitism attempts by drongos, despite wide variation in success according to babbler group size, suggests that kleptoparasitic behavior in this species is fixed, similar to that observed in roseate terns (*Sterna dougallii*), (Shealer et al. 2005). However, to empirically test the assumptions of current theoretical models, it remains to be determined how long drongos are willing to wait for an opportunity to steal food before reverting to self-foraging techniques or transferring to more easily exploitable species. Manipulation of the ratio of true/false drongo alarm calls and the consequent effect on babbler responsiveness and aggression toward drongos would be useful in determining what level of false-calling and kleptoparasitism will be tolerated before drongos are chased off even by small babbler groups. Future experiments to investigate whether pied babblers are willing to accept a higher level of kleptoparasitism when perceived predator risk is high and whether drongos are able to capitalize on changes in babbler behavior will serve to further determine the level of behavioral adjustment in this relationship.

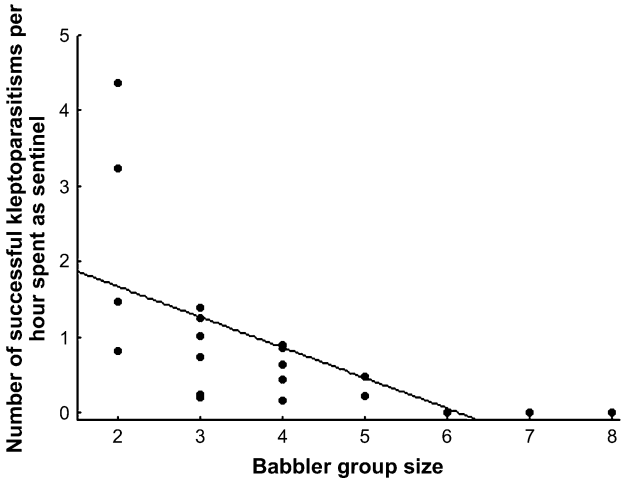

Figure 5
The number of successful kleptoparasitisms achieved by drongos per hour spent vigilant above babbler groups in relation to babbler group size. The line of best fit is generated from the predictions of the GLMM presented in Table 5.

The pied babbler–drongo interaction represents one of the first examples of a facultative response by a cooperative breeder to the presence of a kleptoparasitic species. Behavioral adjustment to such a degree during interspecific interactions has been observed in only one other cooperative breeder, the dwarf mongoose (*Helogale parvula*, Rasa 1983). In this species, individuals spent less time vigilant when hornbills (*Tockus deckeni* and *Tockus flavirostris*) were present and responded strongly to hornbill alarm calls, but there was no evidence of a facultative change in mongoose response to hornbills according to group size (Rasa 1983). The response of babblers to drongos occurs in a variable yet predictable pattern based on need; as group size changes, there is a dynamic change in babbler response to drongo presence.

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