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Specific targeting of host individuals by a kleptoparasitic bird

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Abstract Kleptoparasitism is a tactic used to acquire food opportunistically and has been shown to provide several benefits, including greater food intake rate and the acquisition of items not normally available during self-foraging. Host individuals may differ in their ability to defend themselves against kleptoparasitic attacks and therefore identifying those host individuals that are particularly vulnerable to attack could both provide energetic benefits and increase the efficiency of kleptoparasitism as a foraging strategy. Here, we show that the kleptoparasitic fork-tailed drongo (*Dicrurus adsimilis*) specifically targets juveniles when following groups of cooperatively breeding pied babblers (*Turdoides bicolor*). Drongos give alarm calls upon sighting a predator, thus providing extra predator vigilance to foraging pied babblers. However, drongos also use alarm calls to steal food items. During kleptoparasitic attacks, drongos give false alarm calls and then swoop down to steal food items dropped by alarmed babblers. Juvenile pied babblers are particularly vulnerable to attack because they (a) spend a longer period handling prey items prior to consumption and (b) respond to alarm calls primarily by immediately moving to cover, in contrast to adults who respond by looking up and visually scanning the surrounding area. Drongos attack juvenile babblers significantly more often than adults, with attacks on juveniles more likely to result in the successful procurement of a food item. This patterns of attack suggests that drongos are able to differentiate between individuals of different age when targeting pied babblers, thus increasing the efficiency of kleptoparasitism as a foraging strategy.

Keywords Kleptoparasitism · Fork-tailed drongo · Pied babbler · Targeting behaviour · Alarm call response

Introduction

Kleptoparasitism, where individuals attempt to steal food captured by others, is a foraging strategy widespread among a variety of avian species from a diverse range of taxa and can occur during both intra- and interspecific interactions (Brockmann and Barnard 1979; Morand-Ferron et al. 2007). The costs versus benefits of kleptoparasitism are commonly thought to determine the occurrence of this behaviour relative to the frequency of self-foraging attempts (Giraldeau and Caraco 2000). It has been suggested that kleptoparasites require skills to select appropriate hosts (in terms of behaviour and vulnerability) on which to target attacks as well as skills with which to launch an effective attack while minimising the risk of injury from aggressive response (Brockmann and Barnard 1979; Shealer et al. 1997; Morand-Ferron et al. 2007). To make kleptoparasitism an effective foraging strategy, kleptoparasites should therefore benefit from being able to determine which individuals in a host population are either most vulnerable to attack, the most profitable producers, or the least likely to cause injury to the attacker. Previous research has provided evidence that kleptoparasites tend to target certain individuals, including those that use a foraging strategy with a longer handling time (e.g. the behaviour of dunking food in water by Carib

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grackles, *Quiscalus lugubris*, to speed up ingestion prolongs the exposure of captured items to kleptoparasitism, Morand-Ferron et al. 2006), and individuals that are more successful at finding prey (Shealer et al. 1997).

Kleptoparasitism is likely to be most profitable when individuals are able to use this strategy to capture larger or more nutritionally valuable items at a greater rate than they would be able to during self-foraging (Morand-Ferron et al. 2007). For example, fork-tailed drongos (*Dicrursus adsimilis*) are primarily aerial foragers that catch small winged prey, but they also use false alarm calls to kleptoparasitise large subterranean prey items from terrestrially foraging species such as pied babblers (*Turdoides bicolor*; Ridley and Raihani 2007). The size of the prey items that fork-tailed drongos capture via kleptoparasitism are on average three times larger than those captured during self-foraging (Child 2006). However, profitability will also depend on the ability of kleptoparasites to regularly acquire prey. Due to the fact that host populations may either (a) be spread over a considerable area during foraging, (b) occur in densities that make it difficult to monitor all individuals closely or (c) develop defences against repeated attack, kleptoparasites are likely to benefit from being able to determine which host individuals are most profitable for targeted attacks rather than monitoring an entire foraging group.

It has been well documented in both birds (Marchetti and Price 1989; Wunderle 1991; Yoerg 1994; Rutz et al. 2006) and mammals (Bionski and Fragaszy 1989; Altmann 1988) that there is an ontogenetic shift in foraging efficiency, with adults significantly better at accessing high-quality food resources than juveniles or newly weaned/fledged young. Among cooperatively breeding species in particular, foraging ability has been found to develop relatively slowly (Heinsohn 1991; Langen 1996, 2000). Not only do youngsters require an extended period of time for the acquisition of skills to effectively handle prey (Caro 1980; Thornton and McAuliffe 2006) but they also tend to be relatively poorer at defending resources compared to adults (Zack and Stutchbury 1992; Calsbeek and Sinervo 2002). The greater time spent handling prey prior to consumption means that prey is exposed for longer and hence more vulnerable to kleptoparasitic attack. For example, evidence from the cooperatively breeding meerkat (*Suricata suricatta*) suggests that pups are initially very poor at handling prey items and take considerable periods of time to consume prey that has not been modified or broken down for them by adult group members (Thornton and McAuliffe 2006) and this may explain why fork-tailed drongos primarily target young meerkats for kleptoparasitic attack (T.P. Flower, *unpublished data*).

It is likely that the individuals of a host population most vulnerable to attack will depend on the strategy of kleptoparasitism used. The fork-tailed drongo uses a strategy that may be best described as ‘stealth kleptoparasitism’, defined by Giraldeau and Caraco (2000) as where the kleptoparasite surprises the host and steals the food item before the host can react to the attack. Upon capture of a large food item by a pied babbler, drongos have been demonstrated to give a false alarm call, causing the babblers to flee to cover and allowing the drongo to swoop down and steal food items dropped after the alarm call was given (Ridley et al. 2007). Since previous research has found that young animals in social groups take a while to learn the information encoded in different alarm calls (Seyfarth and Cheney 1986; Hauser 1988; Griesser and Ekman 2005; Hollen and Manser 2006), drongos may be most likely to profit from targeting youngsters when following social species such as pied babblers. This is because (a) youngsters may not be able to differentiate between drongo true and false alarm calls or (b) youngsters may use the default ‘safe’ behaviour of responding to all alarm calls until they develop greater distinguishing ability. In this paper, we aim to determine patterns of kleptoparasitism in relation to attributes of the host population. First, we ask whether fork-tailed drongos target certain individuals in the pied babbler population during kleptoparasitic attack. We then look at whether there are particular attributes of these individuals that make them most profitable for attack including (a) foraging efficiency, (b) handling time of prey items and (c) responsiveness to alarm calls. We discuss the implications of these findings for the profitability of kleptoparasitism as a foraging technique.

Methods

Study site and population

We studied drongo–babbler interactions at ten groups of pied babblers in the Kuruman River Reserve, southern Kalahari Desert, South Africa (26°58′S 21°49′E) between April and July 2007. The study area is semi-arid grassland and acacia savanna, with an average annual rainfall of 217 mm (for a detailed description of the climate and vegetation, see Raihani and Ridley 2007). All pied babblers and drongos at the study site were individually recognisable by a unique combination of colour rings, and were habituated to observation from a distance of approximately 2 to 3 m (for details of the habituation process, see Ridley and Raihani 2007).

Pied babblers are medium-sized passerines (75–95 g) occupying the semi-arid savanna regions of southern Africa. Groups defend year-round territories and forage closely together throughout the day. Pied babblers are primarily terrestrial foragers (more than 95% of foraging time spent on the ground), using their bills to dig in the substrate for prey (Ridley and Raihani 2007). As a consequence, they cannot forage and remain as vigilant for predators as raised sentinels (Hollen et al. 2008). Foraging babblers therefore rely on alarm calls from sentinels to alert them to the presence of predators (Ridley and Raihani 2007). Babbler group size during the study period ranged between two and 12 individuals, averaging 3.5±0.4 (range 2–7) adults (individuals greater than 12 months old) and 2.9±0.6 (range 0–6) juveniles (individuals between 0 and 12 months post-fledging) per group. Juveniles continue to receive some food from adults for 2–3 months post-fledging, but only prey items caught through self-foraging were considered in the following analyses.

Drongos (45–65 g) are solitary foragers that occasionally invest in interspecific kleptoparasitic behaviour, stealing food items from many small to medium-sized bird and mammal species (Hockey et al. 2005). Individual drongos often follow babbler groups, perching above the group and moving between foraging sites with them. When drongos are following babbler groups, they commonly do not forage for themselves, but upon capture of a 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 (Ridley and Raihani 2007). Drongos also regularly give reliable alarm calls upon sighting a predator, and have been observed to mob or physically attack predators approaching babbler groups (Ridley and Raihani 2007). This extra anti-predator vigilance provided by drongos allows pied babblers to reduce personal vigilance time and spend more time foraging, thus providing a benefit of drongo presence (Ridley and Raihani 2007).

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 (Ridley et al. 2007). 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 (Ridley and Raihani 2007). A drongo alarm call that was not immediately followed by an attack for food was not considered false even if no predator was visible. Drongos commonly perched above and followed particular babblers (defined as being 0–3 m from and actively following the individual between foraging sites) within a foraging group (>70% of observation time), rather than perching above the babbler group as a whole.

Data collection

Each babbler group was observed for a minimum of 3 h per day (starting at dawn when the group left the roost tree) twice a week. We collected data *ad libitum* using handheld data recorders on babbler response to drongo alarm calls and the occurrence of kleptoparasitism attempts. For each kleptoparasitism attempt, we noted drongo and babbler identity, prey item size and outcome of attempt (success or fail).

The distance of the drongo to the closest foraging babbler, as well as the identity of the babbler being followed, was recorded each time the drongo changed position. To determine whether differences in handling time may affect which individuals are targeted by drongos, we conducted 20-min time–activity focals (Altmann 1974) on each babbler in the population (average number of focals per individual over whole study period=7.4±0.5, n=575 focals) once a week. Handling time was defined as the period of time from capture of an item to complete consumption or abandonment of the item and was measured to the nearest second. Prey items caught by babblers ranged in size from very small arthropods to large invertebrates and small vertebrates (such as scorpions and lizards). All prey items were assigned a size category, allowing the biomass (g) of each item to be determined (see Raihani and Ridley 2007 for a classification of each size category). Each size category was assigned an average wet biomass value (g) derived from weighing 50 prey items representative of that category.

To determine which individuals responded most strongly to alarm calls, we recorded the response of each group member each time an alarm call was given. Responses were coded as: (1) no response; (2) responds by alerting, lifting head and scanning the surrounding area; and (3) responds by moving to cover. We also recorded the order of response: individuals were coded either as the first, second, third or subsequent group member to respond to an alarm. Where two individuals responded simultaneously, they were assigned the same order of response. For these observations, two observers were present at each group and each assigned half of the group members to observe, to ensure that all individuals could be monitored effectively for type and speed of response. Since the response to predator alarms may vary based on perceived risk and distance from the group, analysis was confined to predators that were less than 100 m from the group at the time of alarm (for a list of predators at the study site, see Ridley and Raihani 2007).

Sexing

Because it was not possible to determine sex from external characteristics in pied babblers, small blood samples (50 µl) were collected from all individuals via brachial venipuncture. Nuclear DNA was extracted, and polymerase chain reaction-based molecular sex determinations were conducted using the method described in Griffiths et al. (1998).

Analyses

Data were analysed using GLMMs (generalised linear mixed models) and LMMs (linear mixed models) in Genstat 10.1 (Genstat 10th Edition, Lawes Agricultural Trust, Rothamsted, UK), which allow terms with repeated measures to be fitted as random terms, thus controlling for non-independence of data. The method of fitting mixed models to data followed Crawley (2002). Model simplification using backward elimination was adopted. Terms were systematically removed from each model and only retained if their removal resulted in a significant loss of explanatory power (the minimal model). The *P* value for eliminated terms was determined by adding each individually to the minimal model. All two-way interactions were tested, but only presented if significant. Throughout the text, means are expressed with standard errors and null hypotheses are rejected at $\alpha<0.05$.

Targeting

To determine whether drongos targeted particular individuals in the study population for kleptoparasitic attack, we looked at the proportion of all kleptoparasitism attempts observed at each group per month that were received by each individual babbler in a LMM with an identity link function. We then looked at whether kleptoparasitism attempts were more likely to be successful according to particular characteristics of the host babbler. For this second analysis, we considered only those individuals who experienced a kleptoparasitic attack. The number of kleptoparasitic attacks that each babbler suffered that was successful (i.e. the food item was lost to the attacking drongo) was used as the response term with the total number of attacks suffered by each individual set as the binomial total in a GLMM with a binomial distribution and logit link function. For both models, age (months post-hatching), sex, foraging efficiency and the group adult: juvenile ratio were included as predictor terms. Babbler, drongo and group identity were included as random terms. Analysis was conducted on 272 kleptoparasitism attempts (of which 71 were successful) observed at ten different babbler groups (*n*=73 babblers, 36 of which suffered a kleptoparasitic attack).

Handling time

Since drongos primarily attempted to kleptoparasitise medium- to large-sized prey items (98.9% of 272 observed kleptoparasitism attempts), handling time analyses were restricted to these prey size classes. For each size class (medium and large) we used average handling time for each individual during each 20-min focal as the response variable and babbler age (months post-hatching), group

Table 1 GLMM analyses of (a) the terms affecting the number of kleptoparasitism attempts on each individual babbler as a proportion of all kleptoparasitism attempts per group per month and (b) the terms affecting the proportion of all kleptoparasitism attempts on each individual that were successful

Model term	Wald statistic	*df*	*P*	Average effect	s.e.
(a) Kleptoparasitism attempts					
Minimal model					
Constant				−1.96	0.16
Age	9.93	1	0.002	−0.03	0.01
Full model					
Foraging efficiency	3.24	1	0.079	2.57	1.46
Group adult:juvenile ratio	1.06	1	0.302	0.11	0.12
Babbler sex	0.37	1	0.541		
Male				0.0	0.0
Female				0.23	0.29
Variance components: group identity 0.19±0.19; babbler identity 0.74±0.28; drongo identity 0.08±0.13					
(b) Successful steals					
Minimal model					
Constant				−1.04	0.22
Age	7.23	1	0.009	−0.05	0.02
Additional terms tested					
Foraging efficiency	1.82	1	0.182	−2.51	1.80
Group adult:juvenile ratio	0.54	1	0.464	−0.32	0.28
Babbler sex	0.34	1	0.560		
Male				0.0	0.0
Female				−0.08	0.32
Variance components: group identity 0.07±0.16; babbler identity bound; drongo identity 0.04±0.22					

Analysis was conducted on (a) 272 kleptoparasitism attempts by 17 drongos at ten different babbler groups over 3 months, incorporating (b) 71 successful steals. Group, babbler and drongo identity were included as random terms in each model

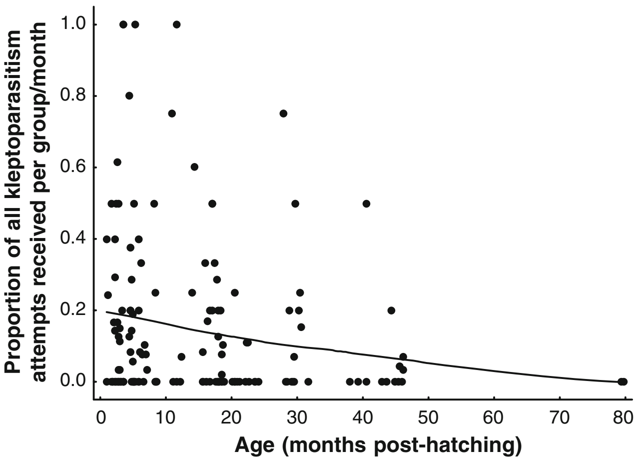

Fig. 1 The relationship between pied babbler age (months post-hatching) and the proportion of all kleptoparasitism attempts by drongos per group per month that were directed at each babbler individual. Raw data values are displayed. The line of best fit is generated from the predictions of the model presented in Table 1

size (all individuals combined) and rainfall in the previous 2 months (since there is often a protracted period of time between rainfall and increased insect abundance, Cumming and Bernard 1997) as predictor terms in a LMM with an identity link function. Group and individual identity were included as random terms in each model.

Alarm call responses

To determine whether there was a difference in alarm-call responsiveness between individuals, we conducted an analysis on factors affecting delay of response. Previous research on this system has indicated that drongo false and true alarm calls are acoustically identical (Ridley et al. 2007) and thus the response of babblers to these different alarm calls is likely to be similar. We used the proportion of all true (i.e. when a predator was present) drongo alarm calls given at each group that each individual was the first to respond to as the response variable in a LMM with an identity link function. Babbler age (months post-hatching), sex and group adult:juvenile ratio were set as predictor variables, and group identity was included as a random term.

Results

Drongos were more likely to successfully kleptoparasitise babblers when following particular individuals than when perched above the group as a whole (36.1% of attempts when following specific individuals were successful, compared with only 11.5% of attempts when not following specific individuals). Drongos attempted to steal food from juvenile babblers more often than adults (Table 1a, Fig. 1), despite juveniles having significantly lower foraging success (juveniles=0.12±0.01 g/foraging min, adults=0.27±0.02 g/foraging min, LMM χ^2=38.86, $P<0.001$). Of 272 observed kleptoparasitism attempts, 54.4% were on juveniles, despite these individuals comprising only 42.8% of the study population. Overall, 24.7% of kleptoparasitism attempts ended in a successful steal. Attacks on younger babblers were more likely to be successful (Table 1b, Fig. 2). For juveniles, 32.7% of kleptoparasitic attacks ended in a successful steal, compared with only 12.6% of attacks on adult birds. The likely reason for this higher success was a poorer ability to handle prey items by young babblers (Table 2), who spent significantly longer handling medium and large-sized prey items prior to consumption (141.1±10.0 s) compared with adults (73.2±3.9 s, Fig. 2a, b), resulting in their prey being exposed to potential kleptoparasitic attack for longer periods.

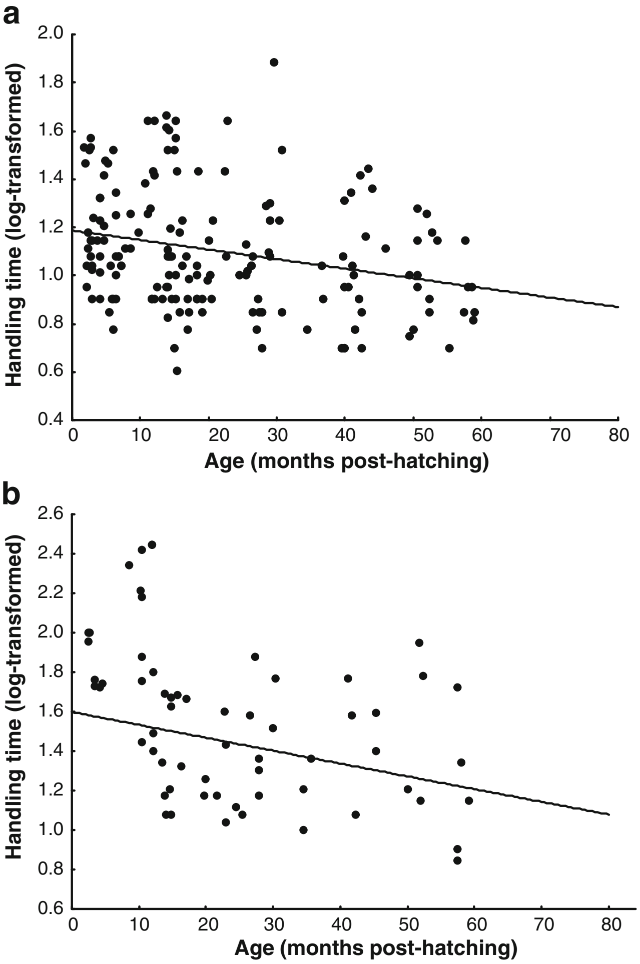

Fig. 2 The relationship between age and handling time for **a** medium- and **b** large-sized prey items for each babbler in the study population. Log-transformed data values are displayed. The line of best fit is generated from the predictions of the LMM presented in Table 2

Table 2 LMM analyses of the terms affecting handling time for medium- and large-sized prey items caught by foraging babblers

Model term	Wald statistic	*df*	*P*	Average effect	s.e.
(a) Medium prey items					
Minimal model					
Constant				1.09	0.02
Age	13.55	1	<0.001	−0.01	1.0×10^{-3}
Additional terms tested					
Sex	0.76	1	0.389	0.0	0.0
Male				−0.03	0.04
Female					
Total rainfall in prior 2 months	0.26	1	0.609	0.02	0.04
Group adult:juvenile ratio	0.09	1	0.768	0.11	0.19
Variance components: group identity 0.01±0.01; babbler identity −0.01±0.02					
(b) Large prey items					
Minimal model					
Constant				1.44	0.03
Age	9.26	1	0.009	−0.01	7.6×10^{-3}
Additional terms tested					
Babbler sex	0.42	1	0.530	0.0	0.0
Male				0.05	0.08
Female					
Group adult:juvenile ratio	0.26	1	0.608	0.12	0.19
Total rainfall in prior 2 months	0.07	1	0.787	0.04	0.11
Variance components: group identity −0.01±0.02; babbler identity −0.01±0.01					

Group and individual identity were included as random terms in each model

Juvenile babblers also displayed a greater responsiveness to alarm calls. Out of 390 alarm calls that we were able to record individual responses for, juveniles accounted for 74.9% (*n*= 140) of all first responses (Table 3, Fig. 3). Whereas adults primarily responded with head-up aerial scans of the surrounding area (62.1% of adult initial alarm call responses, *n*=176 responses), the response of young babblers was primarily to immediately stop foraging or drop their food item and seek cover in the nearest vegetation (67.8% of juvenile initial alarm call responses, *n*=214 responses).

Overall, the number of successful kleptoparasitic attacks on each individual babbler was low (0.46±0.11 successful attacks/juvenile babbler/observation hour, range 0–4.44, compared with 0.19±0.07 successful attacks/adult babbler/observation hour, range 0–3.32). Since attacks were primarily for medium or large prey items, such attacks were likely to be more costly for juveniles owing to their poorer foraging efficiency. The loss of foraging time based on average attack rates and babbler foraging efficiency averaged 2.47±0.62 foraging minutes for juveniles and 0.45±0.29 foraging minutes for adults.

Discussion

Fork-tailed drongos target young individuals for the majority of their kleptoparasitic attacks on pied babblers.

Table 3 LMM analysis of the terms affecting the proportion of all alarm calls given that an individual was the first in the group to respond to

Model term	Wald statistic	*df*	*P*	Average effect	s.e.
Minimal model					
Constant				−0.96	0.25
Age	21.67	1	<0.001	−0.05	0.01
Additional terms tested					
Group adult:juvenile ratio	0.01	1	0.924	−0.03	0.31
Babbler sex	0.01	1	0.911		
Male				0.0	0.0
Female				0.04	0.32
Variance components: group identity 0.14±0.18; babbler identity 0.35±0.53					

Analysis was conducted on the responses by a total of 66 babblers (33 adults, 33 juveniles) to 390 alarm calls given at ten different babbler groups. Group and individual identity were included as random terms in the model

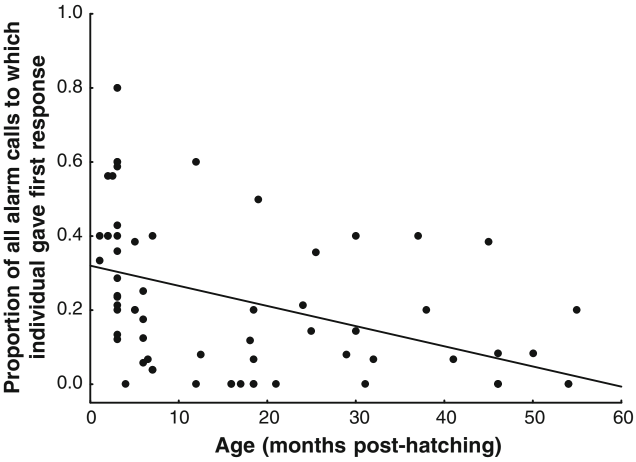

Fig. 3 The relationship between age and the delay in response to alarm calls. Data values are displayed as the proportion of all alarm calls given at each group that each individual babbler was the first to respond to. The line of best fit is generated from the predictions of the LMM presented in Table 3

This targeting behaviour seems to increase the efficiency of kleptoparasitism as a foraging tactic, with attacks on youngsters more likely to result in a successful steal than attacks on adults. Young babblers display particular characteristics that make them vulnerable to kleptoparasitic attack, with a reduced ability to handle prey items compared to adults, similar to patterns observed in other avian species (Heinsohn 1991; Wunderle 1991). The significant amount of time spent handling prey items prior to consumption results in prey being exposed for a considerably longer time period. This may make it more likely that drongos will (a) notice item capture and (b) find time to launch an attack on a juvenile compared to an adult individual.

Drongos target juveniles despite the fact that adults have greater foraging efficiency and hence are more effective ‘producers’ of medium and large prey items. This is in contrast to findings in other kleptoparasitic studies, where kleptoparasites targeted the best foragers in the population. For example, in brown pelicans (*Pelecanus occidentalis*), kleptoparasites were found to target adults (who tended to have higher foraging success than juveniles) more often (Shealer et al. 1997). There are several possible reasons for the difference in these results. First, there is a marked difference in the handling time of juvenile and adult pied babblers, unlike the brown pelican, where no difference was detected (Shealer et al. 1997). Second, adult babblers may be more difficult to attack. Unlike juveniles, who immediately respond to all alarm calls by moving to cover, adults commonly scan the surrounding area after an alarm call is given. This apparent ontogenetic shift in response to alarm calls has been recorded in a number of other species (Seyfarth and Cheney 1986; Griesser and Ekman 2005), and such behaviour makes it more likely that false alarm calls will be detected, making successful kleptoparasitic attacks on adults more difficult. In addition, previous research has shown that older individuals tend to be better at defending resources (Holekamp and Smale 1998). These factors combined suggest that targeting young babblers may be a more profitable strategy for the fork-tailed drongo.

It is as yet unclear how drongos are able to identify which individuals are particularly vulnerable, but previous research in other kleptoparasitic species suggests that this is an acquired skill, with juveniles often making ‘identity errors’ and consequently suffering very low rates of success (Skorka and Wojcik 2008). Young pied babblers have a uniformly brown plumage that becomes mottled with age, and only develops into the fully adult pied plumage by 12 months of age. Drongos may use this difference in plumage to identify young individuals within a foraging group, but this possibility remains to be determined.

Optimal foraging theory (MacArthur and Pianka 1966; Schoener 1971) suggests that animals should employ foraging tactics to maximise their energy intake rate per unit time. By specifically targeting those individuals that take longer to handle prey and are more vulnerable to attack, kleptoparasites may increase the efficiency and value of kleptoparasitism as a foraging strategy. Few studies have simultaneously examined how and why kleptoparasites attack their hosts, and the kleptoparasite–host interaction described here suggests that kleptoparasites use several different methods to maximise the efficiency of attack based on the behaviour of their host species. Further research, indicating (a) whether drongos cease kleptoparasitism of pied babblers when there are few youngsters available to target and (b) whether repeated targeting of the same individual leads to greater resistance to attack, will help to elucidate the dynamics of host switching and kleptoparasitism as a foraging strategy in the fork-tailed drongo.

Detailed research into kleptoparasite–host interactions can provide important information on the evolution of kleptoparasitism because it focuses on a behaviour that is considered to be cognitively demanding (Morand-Ferron et al. 2007). Through their research, Morand-Ferron et al. (2007) suggested that kleptoparasitism has more frequently evolved in lineages with large brains relative to body size. Drongos are a member of the Corvidae family and have a large residual brain size (D. Sol, *unpublished data*). This information, combined with evidence of strategic alarm calling and kleptoparasitism in other drongo species in southeast Asia (Goodale and Kotagama 2006), supports the view that a larger brain may support the development of this type of foraging strategy, and thus further research into the cognitive demands of kleptoparasitism may prove rewarding in this respect.

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References

Altmann J (1974) Observational study of behaviour: sampling methods. Behaviour 49:227–267

Altmann SA (1988) Foraging for survival: yearling baboons in Africa. University of Chicago Press, Chicago

Bionski S, Fragaszy DM (1989) The ontogeny of foraging in squirrel monkeys. Anim Behav 37:415–428

Brockmann HJ, Barnard CJ (1979) Kleptoparasitism in birds. Anim Behav 27:487–514

Calsbeek R, Sinervo B (2002) The ontogeny of territoriality during maturation. Oecologia 132:468–477

Caro TM (1980) Effects of the mother, object play and adult experience on predation in cats. Behav Neur Biol 29:29–51

Child, M.F. 2006. Cunning kleptoparasitism: dynamic strategies to obtain food rewards in a terrestrial system. Honours thesis, University of Cape Town

Crawley MJ (2002) Statistical computing: an introduction to data analysis using S-plus. John Wiley & Sons Ltd., Chichester, UK

Cumming GS, Bernard RTF (1997) Rainfall, food abundance and timing of parturition in African bats. Oecologia 111:309–317

Giraldeau LA, Caraco T (2000) Social Foraging theory. Princeton University Press, Princeton

Goodale E, Kotagama SW (2006) Context-dependent vocal mimicry in a passerine bird. Pro Roy Soc B 273:875–880

Griesser M, Ekman J (2005) Nepotistic mobbing behaviour in the Siberian jay *Perisoreus infaustus*. Anim Behav 69:345–352

Griffiths R, Double MC, Orr K, Dawson JG (1998) A DNA test to sex most birds. Mol Ecol 7:107–1075

Hauser MD (1988) How infant vervet monkeys learn to recognise starling alarm calls: the role of experience. Behaviour 105:187–201

Heinsohn RG (1991) Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. Am Nat 137:864–881

Hockey PAR, Dean WRJ, Ryan PG (eds) (2005) Robert's birds of Southern Africa, 7th edn. The Trustees of the John Voelcker Bird Fund, Cape Town

Holekamp KE, Smale L (1998) Behavioral development in the spotted hyena. Bioscience 48:997–1005

Hollĕn LI, Manser MB (2006) Ontogeny of alarm call responses in meerkats, *Suricata suricatta*: the roles of age, sex and nearby conspecifics. Anim Behav 72:1345–1353

Hollĕn LI, Bell MBV, Radford AR (2008) Cooperative sentinel calling? Foragers gain increased biomass intake. Curr Biol 18:576–579

Langen TA (1996) Skill acquisition and the timing of natal dispersal in the white-throated magpie-jay, *Calocitta formosa*. Anim Behav 51:575–588

Langen TA (2000) Prolonged offspring dependence and cooperative breeding in birds. Behav Ecol 11:367–377

MacArthur RH, Pianka ER (1966) On the optimal use of a patchy environment. Am Nat 100:603–609

Marchetti K, Price T (1989) Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. Biol Rev 64:51–70

Morand-Ferron J, Veillette M, Lefebvre L (2006) Stealing of dunked food in Carib grackles (*Quiscalus lugubris*). Behav Proc 73:342–347

Morand-Ferron J, Sol D, Lefebvre L (2007) Food stealing in birds: brains or brawn? Anim Behav 74:1725–1734

Raihani NJ, Ridley AR (2007) Adult vocalizations during provisioning: offspring response and post-fledging benefits. Anim Behav 74:1303–1309

Ridley AR, Raihani NJ (2007) Facultative response to a kleptoparasite by the cooperatively pied babbler. Behav Ecol 18:324–330

Ridley AR, Child MF, Bell MBV (2007) Interspecific audience effects on the alarm-calling behaviour of a kleptoparasitic bird. Biol Lett 3:589–591

Rutz C, Whittingham MJ, Newton I (2006) Age-dependent diet choice in an avian top predator. Proc Roy Soc B 273:579–586

Schoener TW (1971) Theory of feeding strategies. Ann Rev Ecol Syst 2:369–404

Seyfarth RM, Cheney DL (1986) Vocal development in vervet monkeys. Anim Behav 34:1640–1658

Shealer DA, Floyd T, Burger J (1997) Host choice and success of gulls & terns kleptoparasitizing brown pelicans. Anim Behav 53:655–665

Skorka P, Wojcik JD (2008) Habitat utilisation, feeding tactics and age-related feeding efficiency in the Caspian Gull *Larus cachinnans*. J Ornith 149:31–39

Thornton A, McAuliffe K (2006) Teaching in wild meerkats. Science 313:227–229

Wunderle JM (1991) Age-specific foraging proficiency in birds. Curr Ornith 8:273–324

Yoerg SJ (1994) Development of foraging behaviour in the Eurasian dipper, *Cinclus cinclus*, from fledging until dispersal. Anim Behav 47:577–588

Zack S, Stutchbury BJ (1992) Delayed breeding in avian social systems; the role of territory quality and "floater" tactics. Behaviour 123:194–219