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Kleptoparasitism in the Balearic lizard, *Podarcis lilfordi*

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Kleptoparasitism is taking food from another individual, which may be a conspecific or member of another species. Among squamate reptiles intraspecific kleptoparasitism is very often observed in captives housed at high density, but is noted much less often in

the field. At low population density, kleptoparasitism must be rare, but high population density provides frequent opportunities (Ruxton and Moody, 1997; Triplet et al., 1999). Little is known about kleptoparasitism by lizards in the field, but this form of interference competition occurs frequently in the cordylid lizard *Platysaurus broadleyi* (formerly *capensis*) when feeding on figs (Whiting and Greef, 1997). At Augrabies Falls National Park these lizards occur at high density near the Orange River where insects, especially flies, are very abundant and fig fruits are periodically abundant (Whiting and Greef, 1997).

Two conditions favoring kleptoparasitism are met for *P. broadleyi* near Augrabies Falls: lizards are abundant and food must be processed for a relatively lengthy period before being swallowed. Handling times for figs were more than a half minute for males and more than a minute for females (Whiting and Greef, 1997). Nearly one third of lizards having obtained figs were approached by other individuals that attempted to steal the food, with a mean of slightly less than one individual approaching each feeding lizard (Whiting and Greef, 1997). The staple food of *P. broadleyi* at Augrabies Falls, a small fly, can be swallowed quickly, allowing very little opportunity for kleptoparasitism.

Faced with conspecifics attempting to steal food, lizards may respond by running away with the food, decreasing handling time, or both. If food is too large to permit rapid carrying, it might be defended against one or a few conspecifics. Alternatively, several individuals might feed simultaneously on a large food item, as do Komodo dragons feeding on large carcasses (Auffenberg, 1981). Responses to kleptoparasites might also depend on the likelihood that the kleptoparasite will be able to steal the food. Attempts to steal figs by *P. broadleyi* were successful in slightly over 10% of observations (Whiting and Greef, 1997), indicating that this species has fairly effective defenses against fig theft.

Here we report the findings of field experiments on kleptoparasitism in the Balearic lizard, *Podarcis lilfordi*, from Aire, an islet offshore from Menorca, Balearic Islands, Spain (elevation 0-15 m). *Podarcis lilfordi* is an omnivorous lacertid (Pérez-Mellado and Corti, 1993) that reaches extremely high density on Aire and other islets surrounding Menorca, up to 20,000 per hectare (Salvador, 1998). Balearic lizards frequently interact aggressively during the breeding season, but there is no evidence that they are territorial (Pérez-Mellado, 1989). After casually observing attempted kleptoparasitism by lizards feeding on insects and fruit, we studied the frequency and success of interference with feeding on two types of food, the responses to attempted food theft, and the numbers of individuals vying for food items.

We observed *Podarcis lilfordi* on Aire Island in sunny conditions in June, 2000 at air temperatures of 26-28°C between 1100 and 1500 h. The maximum SVL for *P. lilfordi* is ca. 80 mm for males and 75 mm for females (Barbadillo et al., 1999). Males were recognized by their larger head size; juveniles were lizards less than one year old that were markedly smaller than adults of both sexes. After conducting each trial, we moved to a new location to reduce the likelihood of pseudoreplication, but it is possible that some individuals may have been attracted to attempt kleptoparasitism in more than one trial.

In a first experiment we selected a focal individual that was alone or a group of two or more individuals within a 1 m radius. We then tossed a cut piece of pear (*Pyrus communis*) fruit next to (<0.15 m) an individual if it

Table 1. Numbers of individuals of *Podarcis lilfordi* that suffered interference by conspecifics when attempting to eat pieces of pear while alone or in groups and mealworms while in groups, numbers that fled with food, and numbers of trials in which other lizards stole food from the first lizard to bite it.

	Interference		Flee with food		Food stolen	
	Yes	No	Yes	No	Yes	No
Pear						
Alone	0	18	1	17	–	–
Group	22	0	21	1	10	7
Mealworm						
Group	16	7	23	0	0	23

was alone, or to the center of a group. Pear pieces were irregularly shaped wedges with maximum dimension of 15–20 mm. They were too large to be swallowed whole, requiring the lizards to take bites. Straight cut edges allowed lizards to effectively grasp pear pieces in their jaws. We recorded whether the trial tested an individual that was alone or a group, the number of conspecifics in the group, whether or not other individuals attempted to interfere with feeding by the animal that initially grasped the food, the behavior of the initial animal that grasped the food, the age group and sex of group members and the eventual feeder, and the success or failure of attempted food theft. In a second experiment, the food item was a mealworm (larval *Tenebrio molitor*) 29.5 ± 0.3 mm long (mean ± 1.0 s \bar{x}). Trials were conducted and data recorded as in the experiment with pears. In neither experiment was there any indication of species-typical aggression directed to lizards as opposed or in addition to attempts to steal food.

Several differences were assessed for significance using Fisher exact probability tests (Zar, 1996). For each experiment we tested the significance of differences in the probabilities of attempted interference with feeding and of grabbing the food and running by the first lizard to grasp the food for trials involving isolated individuals and groups. We also examined the relationship between group size and success of kleptoparasitic attempts and the significance of the difference in probability of successful food theft between pears and mealworms. Significance tests were two-tailed, with $\alpha = 0.05$.

In tests with pears as food, group size was 4.5 ± 1.0, with range 1–25 ($n = 40$). Individuals were alone in nearly half of trials (18). Because we sampled many such groups to permit assessment of responses to food when no competitors were at hand, they may be overrepresented. The frequencies of larger groups presumably reflect the underlying distribution of group sizes more accurately. The frequencies of the larger group sizes were eight of size two, six of sizes between three and eight, and five of large sizes between 15 and 25. Attempted kleptoparasitism occurred in all trials of groups of two or more individuals (table 1). Interference with feeding occurred significantly more frequently in groups of two or more individuals than in solitary individuals ($P < 1.0 \times 10^{-6}$, table 1), an obvious result that nevertheless highlights the importance of kleptoparasitism and an advantage of being solitary.

In 55% of the groups for which it was possible to ascertain the success of kleptoparasitism when the food was pear, food theft occurred (table 1). In some cases two or more individuals each ate part of the piece of pear. In the five largest groups consisting of 15 or more individuals, it was not possible to determine whether more than one individual obtained part of the food. In all 20 recorded contests over pears, adult males were the winners although females and/or juveniles were present in nine of the groups and juveniles in four. It was not possible to measure SVLs, but it was apparent that the eventual winner was almost always the largest individual in the group or one of the largest. There was a nonsignificant trend for the success of food theft to be greater in larger groups. In groups of two individuals three of eight attempted thefts were successful, whereas in groups of three to eight individuals seven of nine attempts were successful ($P < 0.154$).

Lizards in groups were observed biting each other in fights over pieces of pear in five trials. In all but one of 22 trials in groups, an individual grasped the pears and ran away with them, whereas only one isolated individual did so (table 1). All other solitary individuals ate the pear in situ. Thus, individuals in groups were significantly more likely to grab the food and flee than were isolated individuals ($P < 1.0 \times 10^{-6}$).

In tests with mealworms as food, group size was 3.8 ± 0.3 , with range 2-6 ($n = 23$). Attempted kleptoparasitism of mealworms occurred in 70% of trials, but all attempted thefts failed (table 1). In all trials the first lizard that rushed to the mealworm grabbed it and ran (table 1). Lizards that captured mealworms included 11 males, 11 females, and one juvenile. One male ran a short distance, stopped, and rapidly swallowed the mealworm. Others ran farther, often into bushes, precluding direct observations of feeding. While running, several lizards were chased by other individuals, one of which bit the tail of the lizard holding the food.

Interference in group trials was significantly more likely to be attempted when the food was pear than when it was mealworm ($P = 0.01$). Food theft was more likely to occur in pear than mealworm trials in groups, whether for all trials ($P < 4.6 \times 10^{-5}$) or strictly for trials in which attempts were observed ($P < 0.0005$). Both sexes attempted kleptoparasitism. In trials with mealworms, higher proportions of females alone ($P < 0.0004$) and females plus juveniles ($P = 0.0001$) obtained food than in trials with pears.

Kleptoparasitic competition for food was a very frequent event in the experimental trials. The observed frequency was probably greater than the levels for natural feeding events because food items were introduced from above by tossing them to the lizards, thus affording all lizards a clear view of the food and stimulating them by the food's motion (Whiting and Greef, 1997). Nevertheless, kleptoparasitism occurs naturally and presumably occurs frequently in *P. lilfordi* in areas of high population density.

The selective importance of kleptoparasitism for lizards that find food is underscored by the consistency of attempts to grab the food and escape before eating by lizards in groups fed both pear pieces and mealworms. Lizards in groups fled immediately upon grasping mealworms, even fleeing preemptively when no attempts to steal food had occurred. Such behavior would be unlikely to occur unless a high probability of interference makes it beneficial. It might be objected that lizards in the open might have carried food away to shelter to reduce vulnerability to predation, but this explanation is contradicted by the near absence of such behavior by solitary lizards.

Countermeasures to kleptoparasitism have evolved in diverse taxa and include increased vigilance during food handling (Goss-Custard et al., 1999), adjustment of foraging group size (Norris and Johntone, 1998), and evolution of morphological and behavioral traits such as soldier morphs, early dispersal, and change of microhabitat (Crespi and Abbot, 1999). Rapid dashing to food, fleeing from other individuals while carrying the food, and rapid swallowing as observed in both species of lizards that have been studied (Whiting and Greef, 1997; this paper) are very likely widespread, relatively unspecialized defenses against intraspecific kleptoparasitism.

The importance of kleptoparasitism for *P. lilfordi* that detect other individuals with food is suggested by the very high frequency of attempts to interfere with feeding and by the frequent occurrence of fighting, including biting, over food. The high rate of successful food theft in trials with pears reinforces the hypothesis that kleptoparasitism may be viable means of obtaining food in areas of high population density, especially for large individuals and food types that require substantial processing, prolonging the opportunity for theft. This might apply to large invertebrate prey and perhaps more so to relatively large, tough plant items.

Although lizards in groups regularly attempted to interfere with feeding on both pears and mealworms, they were much more successful in stealing all or part of pear pieces than mealworms. The significantly greater probability that no attempted food theft occurred in a trial with mealworms than with pear pieces appeared to be a consequence of the ease of capturing a mealworm, running away quickly, and swallowing rapidly. This often occurred so quickly that there was very little opportunity for kleptoparasitism, accounting for the observation that the first lizard to reach a mealworm ate it in all trials. In trials with the larger pears, the lizards had more difficulty grasping the food, allowing other individuals more time to interfere. The difficulty of handling and large size of pear pieces may have prevented females and juveniles from grasping them and escaping before larger male competitors arrived to steal the food, explaining the finding that large adult males obtained all of the pears. Females and juveniles were able to grasp and flee with the smaller mealworms, accounting for the significantly greater proportion of females and juveniles that avoided food theft in trials with mealworms than with pears. Further work is needed to define the characteristics affecting ease of kleptoparasitism, excluding the possibility that the difference is simply one between plant and animal food.

Because larger groups imply more potential for attempting theft of food, it may be predicted that the rate of successful theft increases with group size. Although there was a trend in this direction for our data in pear trials, the difference in theft rates between groups of two lizards and larger groups was not significant. However, the power of the test was quite low due to small sample size. More data are needed to test the hypothesis.

Food theft is likely to be most frequent in dense populations of lizards such as those of *P. lilfordi* (this study) and *P. broadleyi* (Whiting and Greef, 1997). High density increases opportunity for kleptoparasitism and facilitates rapid data collection. However, kleptoparasitic food theft has received very little attention in lizards and may be more widespread than is currently realized. Although lizards typically occur in populations having much lower densities than *P. lilfordi* and *P. broadleyi*, many species at lower overall density are locally concentrated due to territoriality or social aggregation. The possibility that frequent opportunities lead to kleptoparasitism and countermeasures in such groupings awaits investigation.

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Mucosubstance histochemistry in the esophagus of the lizard *Agama stellio stellio*

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Although numerous histochemical studies have been made on mammalian gastrointestinal mucosubstances (Obuofuribo, 1975; Shehan and Jervis, 1976) and reptilian oral glands (see review by Kochva, 1978) less information is available on the gastrointestinal mucosubstances of reptiles (Luppa, 1977; Ferri and Liquori, 1992). This is a first attempt to