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Do kleptoparasites reduce their own foraging effort in order to detect kleptoparasitic opportunities? An empirical test of a key assumption of kleptoparasitic models

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Smith, R. D., Ruxton, G. D. and Cresswell, W. 2002. Do kleptoparasites reduce their own foraging effort in order to detect kleptoparasitic opportunities? An empirical test of a key assumption of kleptoparasitic models. – Oikos 97: 203–212.

Determining if, or when, individuals trade off time spent personally feeding against time spent monitoring others for kleptoparasitism opportunities is essential to an understanding of the evolution of scrounging and usurpation behaviours. We provide a first field test of whether kleptoparasites reduce their personal foraging effort in situations where the frequency and rewards of kleptoparasitism increase. We provided experimental food patches for wild European blackbirds that varied in the distribution of prey and that had a potentially high rate of kleptoparasitism within pairs of blackbirds feeding in them. Although individuals differed in their rate of kleptoparasitism, they did not vary in the size of the reward that they gained from kleptoparasitism. As prey became more clumped, kleptoparasitism rate and its reward per incident increased on average. There was, however, no evidence that individuals that were kleptoparasitising more quickly and/or at a higher frequency had lower personal foraging effort. In contrast, foraging effort increased in focal birds compared to when they were foraging alone, independent of dominance, kleptoparasitic opportunity or reward. Our evidence suggests that in some circumstances a kleptoparasite can detect kleptoparasitic opportunities without compromising its own personal foraging rate.

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Animals commonly forage in groups. One consequence of feeding in groups is that individuals can observe and take advantage of the food discoveries of others. As a result, an individual finding food may either have to share the food source it has discovered (see Barnard and Sibly 1981), or in the extreme case, may be driven from it by more dominant individuals (kleptoparasitism). There has been intensive theoretical development aimed at understanding the conditions that might give rise to these systems because they will be crucial determining the evolution of group foraging (reviewed in Giraldeau and Beauchamp 1999, Giraldeau and Caraco 2000). A key consideration in the theory of when scrounging and kleptoparasitic systems might arise is the idea that individuals may have to make a significant investment in order to be able to detect opportunities to kleptoparasitise others (Giraldeau and Beauchamp 1999). Specifically, it is suggested that individuals must trade off their ability to detect such opportunities against their own ability to find food themselves (Broom and Ruxton 1997). This is because watching conspecifics and looking for food are likely to involve looking at two separate things; time of perceptual processing effort devoted to watching conspecifics could otherwise be utilised to enhance personal food finding. Empirical evidence for the existence of this trade off is currently lacking (Giraldeau and Beauchamp 1999) apart from a single study that did

Accepted 9 January 2002

ISSN 0030-1299

[illegible] klepto[illegible]aras[illegible]tism and food find[illegible] [illegible] (Coolen et al. 2001). In this [illegible] look for [illegible]ther evidence for the trade-o[illegible] [illegible] kleptoparasitic opportunities and perso[illegible] foraging.

We [illegible] a field [illegible] of [illegible] feeding on the ground [illegible] evidence for the tra[illegible] pe[illegible] foraging and kleptoparasitic effort. [illegible] a good [illegible] to study any trade-[illegible] feeding [illegible] search for food [illegible] which [illegible] the detection of a [illegible] opportunity" ([illegible] 1994). We presented blackbirds with [illegible] patches that varied in the distribution of [illegible] in order to vary kleptoparasitic opportunities. If there is a trade-off between time allocated to [illegible] and time allocated [illegible] detecting kleptoparasitism opportunities, then we would expect [illegible] to [illegible] [illegible] termined that kleptoparasitism was indeed occurring in the [illegible] that as food became more clumped and the potential reward from displacing a [illegible] increased, the frequency of kleptoparasitism [illegible]. We then [illegible] whether the greater use of klepto[illegible]sitism by an individual is correlated with [illegible] personal foraging.

Methods

We [illegible] the feeding behaviour of a population of wintering blackbirds in the grounds of Hope[illegible] House near Edinburgh on 53 days between 5th January and 4th March 2000. This population was individually colour-marked and has been the subject of foraging research each winter since 1994 (Cresswell 1997, 1998[illegible]). Birds were offered patches of shredded suet (cylinders of white fat, approximately 8 mm long and 3 mm in diameter) spread below a layer of autumn leaves. Blackbirds tossed leaves aside to uncover the suet in a similar way to natural foraging [illegible] 1988, see also Cresswell et al. 2001, Smith et al. [illegible]).

We provided [illegible] experimental leaf patch at one of [illegible] locations in approximately 2 ha of parkland. The [illegible] of [illegible] experimental [illegible] patches [illegible] opposed [illegible] by clearing [illegible] approximately 5 [illegible], and [illegible] white pegs [illegible] along the edges of the patches. Only one [illegible] available [illegible] any given [illegible] and consequently [illegible] birds from throughout the study area. After a patch had been depleted, we removed leaves and [illegible] patches before preparing a new patch [illegible] one of the other locations [illegible] acted both as a cue for the presence of [illegible] and the edges of the patches. All patches [illegible] 5 × 0.75 m and the long side was situated [illegible] to thick cover [illegible] (*[illegible]dron*), separated by up to 1 m of open ground. [illegible] birds entered the patches from the [illegible] beyond the outer patches were distant (20–40 m). We collected data from a total of 27 [illegible] individuals. A few other blackbirds fed sporadically in our patches but not sufficiently regularly to provide data. [illegible] birds fed at up to 10 of the 14 locations ([illegible]), whilst each patch [illegible] up to [illegible] (median = 4). There was no [illegible] difference in the patches at which a bird foraged alone and at which that same bird foraged in company.

The benefits of kleptoparasitism were [illegible] over the course of the study by changing the way in which suet was initially distributed within the patch while keeping the overall density of suet [illegible] at one hundred shreds per patch (Table 1). We firstly offered blackbirds kleptoparasitic opportunities by providing suet in clumps of ten shreds (Regime 1). All suet shreds within a clump were placed in [illegible] within an area of approximately 10 [illegible], so that they would generally be completely [illegible] one or two leaves. The purpose of Regime 2 was to remove the opportunity for kleptoparasitism by spreading the hundred shreds uniformly throughout the patch. This was followed by a period in which both uniformly sprinkled suet and clumps of ten shreds were available simultaneously (Regime 3), a further period of [illegible] clumps of [illegible] shreds (Regime 4), and finally a period when [illegible] the benefits of kleptoparasitism [illegible] in [illegible] clumps of 20 suets (Regime 5). Clumps were distributed randomly throughout the leaf patch and patches were regularly replenished during breaks in blackbird feeding.

Table 1. [illegible]

[illegible]	Kleptoparasitism [illegible]	[illegible]	Dates
[illegible]	[illegible]	[illegible] each of 10 clumps	[illegible]
[illegible]	[illegible]	[illegible] shreds spread uniformly	[illegible]
[illegible]	[illegible]	[illegible] three in each of 5 clumps plus [illegible] shreds spread uniformly	[illegible]
[illegible]	[illegible]	[illegible] three in each of 10 clumps	[illegible] 1st February
[illegible]	[illegible]	[illegible] three in each of 5 clumps	22nd February–4th March

Individual blackbirds commonly took between [illegible] and 10 suet shreds during a feeding bout. Feeding [illegible] often lasted several minutes, after which the individual usually returned to [illegible]. All trials were filmed [illegible] a portable camcorder, allowing us to ascertain which blackbirds fed simultaneously, and when they found suet. In order to find suet, blackbirds [illegible] leaves a[illegible] a series of vigorous head movements, interspersed with deliberate jabs to pick up uncovered suet. We recorded the [illegible] timing of [illegible] leaf tosses and suet pecks [illegible] budgets using an event-recording program [illegible] time budgets into periods when birds fed [illegible] other bird. Periods when more than two birds were present were ignored. The layer of leaf litter was shallow and so was unlikely to have obstructed a bird's vision, either of each other or of approaching predators. We could easily distinguish between a blackbird stooping to toss leaves or to pick up suet because the latter was characterised by a more deliberate action, lack of leaf movement and visibility of suet prior to swallowing. Hence it seems reasonable to assume that blackbirds were at least equally as able to detect when other birds found suet when they monitor a foraging companion.

Our measure of personal food searching [illegible] to [illegible] when suet was [illegible] in order to maintain consistency in the [illegible] foraging intensity across the five different feeding regimes and to ensure that [illegible] did not affect our results. We achieved this by calculating the length of time between successive leaf tosses (and [illegible] when tosses were followed by suet-pecks [illegible]). We [illegible] budget as a period of continuous presence in the leaf patch either alone or with the same foraging partner. Periods when three or more birds were present were not included except to measure an individual's overall experience of a new food regime. Time budgets were removed from our analysis if they lasted less than 10 [illegible] included less than five inter-toss intervals (usually [illegible] consuming clumps of suet or spe[illegible] vigilant). Often a single bout of feeding was split among several time budgets [illegible] bird left the patch [illegible] or other [illegible] arrived. In these cases we pooled data from time budgets where the focal bird fed alone or with the same companion, more than once, unless they were separated by periods of at least [illegible].

We hypothesised [illegible] as the benefits of kleptoparasitism increased, potential kleptoparasites would invest more time monitoring the feeding activities of fellow foragers and as a result would spend less time foraging. We therefore needed a quantitative estimate of individual foraging [illegible]. We used the time interval between leaf tosses as a [illegible] measure of foraging effort: those individuals that [illegible] more time to detecting kleptoparasitic [illegible] should either lengthen [illegible] intervals [illegible] of longer intervals. [illegible] however, we noticed that when [illegible] times were [illegible] (approximately [illegible]), these were interspersed [illegible] few [illegible] with longer intervals when individuals lifted their heads [illegible], before resuming [illegible]. Birds [illegible] to usurp other birds [illegible] periods without [illegible] of more than 6 [illegible] we therefore [illegible] inter-toss intervals of more than 6 s [illegible] monitoring in order to take advantage of food [illegible] and therefore removed these from the analysis. Still longer periods without [illegible] were usually associated with "[illegible]ness", [illegible] alarm calls or [illegible] aggression suggesting that these long inter-toss periods were associated with anti-predation vigilance. We therefore use two measures of foraging [illegible] in each time budget. We first calculated median inter-toss intervals for all intervals [illegible]. The second to quantify the length of the [illegible] period when vigilance [illegible] specific [illegible] probably [illegible] to give greater weight to the longer [illegible] periods when the [illegible] was lifted [illegible] between tosses, we calculated the mean [illegible] up to 6 [illegible]. Both [illegible] median and [illegible] mean [illegible] were log 10-transformed prior to their use in [illegible] statistical tests.

Changes in personal [illegible] behaviour associated with changes in kleptoparasitic opportunity were not expected to be instantaneous, but to accumulate as birds became familiar with a new feeding regime. We allowed for this in two ways. Firstly, we omitted data from [illegible] insufficient experience of a new feeding regime. Specifically, as the changes in suet presentation were [illegible] (Table 1), we only omitted data from the [illegible] early part of a bird's feeding [illegible] new feeding regime. Data were omitted if a bird had not found at least five suet clumps in the new feeding regime or, when suet was sprinkled uniformly (Regime 2), had [illegible] than [illegible] feeding in patches. As a [illegible] of temporal effects influencing our [illegible] of personal foraging effort was re-run with Julian date (or equivalently days since the change in regime) as an added factor, but in no case did this improve the fit of the model; [illegible] omit this from our presented results.

Dominance interactions were frequent and mostly consisted of the [illegible] initiator displacing the [illegible] (98% of 467 interactions). [illegible] results were [illegible] consistent throughout the winter allowing us to assign dominance to one of other [illegible] when [illegible] simultaneously. Dominance relationships were assigned [illegible] from interactions that did not involve kleptoparasitism. Of the 336 pairs of birds [illegible] interact, only 57 pairs changed dominance [illegible] during the winter. Thirty-three of these

changes were permanent, i.e. the initial loser was not seen to lose again after its first win. Thirteen of the remaining 24 pairs of birds showed only single reversed wins for the subordinate individual. The remaining 11 contests showed up to ten changes (median = 4), perhaps because birds were closely matched. Dominance relationships were sometimes unknown (if the two contestants were never seen to interact). To ensure maximum parsimony when assigning dominance we only included data from pairs of birds when the same bird was known to have won encounters between them both before and after a feeding event, i.e. feeding data was omitted during the period when a dominance change was occurring.

123 suet clumps were found by subordinate birds, of which 143 (44.0%) were kleptoparasitised. 311 patches were found by dominant birds, of which only 7 (1.6%) were kleptoparasitised. These 7 "reversals" may have occurred as a result of temporary dominance changes, or merely prior to one of when a "usurpation" had occurred. On some occasions the true dominant may merely have just left. We therefore consider kleptoparasite opportunities to be purely the preserve of dominant individuals and subsequently only consider the outcome of the 325 suet clumps found by subordinates. We define the probability that a patch discovered by the subordinate will subsequently usurped by the dominant as the "kleptoparasitic rate". We describe the speed with which the dominant kleptoparasitised subordinate's patch is discovered by the "finder's advantage", defined as the number of items that the subordinate discovers consumed from the patch before the dominant individual kleptoparasitised.

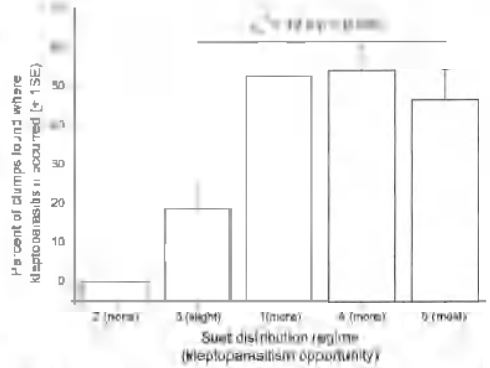

Fig. 1. The change in rate of kleptoparasitism of blackbirds with different distributions of suet in experimental patches. Prey becomes progressively more clumped along the x-axis apart from Regimes 1 and 4 that are the same (see Table 1). A post-hoc Tukey test suggests no difference (at $P < 0.05$) between behaviour in Regimes 1, 4 and 5, but there is between these three and regime 3.

Results

Does the frequency and reward of kleptoparasitism by dominants depend on food distribution?

Discounting the early part of each experimental suet regime, 248 potential kleptoparasitic opportunities were available to 19 individual dominant birds with a median of 9 kleptoparasitic opportunities per bird (range 2–36). We take "individual" as the independent unit of measurement. The mean kleptoparasitic rate amongst the eight birds that had more than six kleptoparasitic opportunities was 44%, but varied significantly between individuals (13–76%; chi-square test: $\chi^2_7 = 31.2$, $P < 0.001$). However, for the absence of cases where kleptoparasitism did occur the speed of kleptoparasitism was similar between individuals (the size of the finder's advantage was not dependent on the identity of the dominant, Kruskal-Wallis test: $\chi^2_7 = 9.4$, $P = 0.23$).

We tested whether dominant individuals would be more likely to take opportunities to kleptoparasitise subordinates when the mean of discovered food patches was greater (e.g. the clumps of 20 suet pieces in regime 5 compared to the patches of 10 in Regimes 1 and 4). We used a log-linear model to examine the relationship between whether a suet clump was kleptoparasitised or not, and two dependent variables: suet regime (4 categories) and bird identity (eight birds with > 10 records as above). There was no evidence of interaction between bird identity and suet regime on the frequency of kleptoparasitism (log-likelihood chi-square test comparing models with and without the interaction: $\chi^2_{21} = 18.2$, $P = 0.59$). After omitting this interaction, both bird identity ($\chi^2_7 = 31.2$, $P < 0.001$) and suet regime ($\chi^2_3 = 13.5$, $P = 0.004$) were found to have significant independent influences on kleptoparasitic frequency.

The rate of kleptoparasitism (percentage of suet clumps found that were kleptoparasitised) was highest in patches where suet occurred only in clumps (Fig. 1). The speed of kleptoparasitism (mean number of suets eaten in a clump by the finder) was not significantly different between the different regimes (Fig. 2a) but the reward of kleptoparasitism was much higher for the usurper in the regime where the suet was most clumped (Fig. 2b). Consequently the mean amount of suets in a clump eaten by the usurper increased significantly as suets become more clumped (Fig. 2c).

Do birds that have a higher rate of kleptoparasitism have a lower personal food searching intensity?

We compared kleptoparasitic frequency and efficiency (as measured by the size of the finder's advantage that varied across suet regimes) with an individual's personal food searching intensity (as measured by mean log (10-sum formula 3 s median or 5 s mean inter toss times). To increase the power of this analysis, we increased the sample size of dominants by using all birds that had five or more kleptoparasitic opportunities (10 or more used in previous section). Overall there was no evidence of a relationship between personal food searching intensity and measures of kleptoparasitism (Table 2). Similar results were obtained if we limited the analysis to individuals with 10+ kleptoparasitic opportunities (as in the last section), and/or adjusted the feeding effort variables for differences in feeding effort between different suet regimes. In contrast to our expectation that personal food searching intensities of dominants would decrease when a subordinate joined the local patch, Table 3 shows that they actually increased (i.e. negative values for d1 and d2 show that inter-toss intervals were lower when birds fed together) indicating a higher individual foraging effort). This may reflect an increased group-size foraging advantage, enabled through shared vigilance.

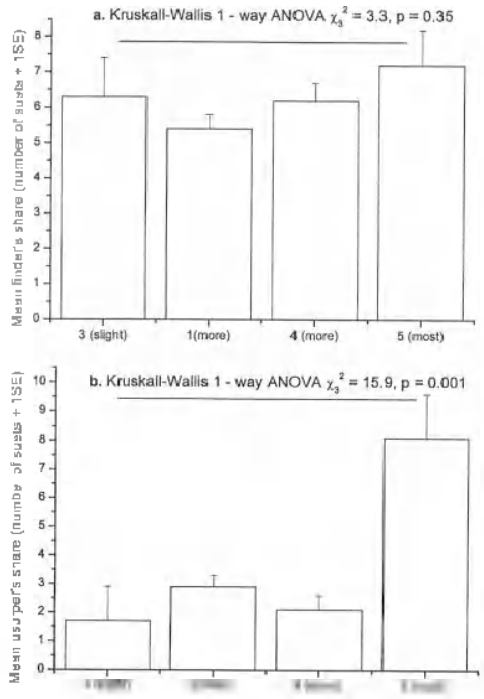

Fig. 2. The usurper's reward of a kleptoparasitic finder's suet clump. The mean reward of a blackbird that kleptoparasitised the suet clump and the percentage of the total suets that were originally available that were eaten by the kleptoparasite with different distributions of suet in experimental patches. Prey becomes progressively more clumped along the x-axis apart from regimes 1 and 4 that are the same (see Table 1). (a) and (c) a post-hoc Tukey test (at $P < 0.05$), finds no difference between behaviour in Regimes 1, 3 and 4 but that all of these three are significantly different from regime 5.

Discussion

As a necessary preliminary to our result, this study clearly demonstrated that kleptoparasitism frequency and reward varied significantly within our system. Broadly as the benefits of kleptoparasitism increased, so did its frequency. That kleptoparasitism rate depends on prey distribution and profitability is well established (Brockmann and Barnard 1979, Barnard 1984, Thompson 1986) although almost all data comes from non-experimental systems. Our initial result is important, however, because our main result is a lack of evidence that foraging effort varied with kleptoparasitism opportunity. It is therefore essential to demonstrate that our study system had a reasonable amount of variation in kleptoparasitism opportunity and benefit, and was therefore a valid one in which to look for evidence for changes in personal foraging effort in response.

As expected, no kleptoparasitism occurred when suet was spread evenly. However, when food was clumped, kleptoparasitism occurred frequently in our system (dominants usurped subordinate finders on 50% of occasions when the latter found suet clumps) and reward (amount of suet clump became larger, interestingly in Regime 3, where suet was sprinkled evenly as well as occurring in clumps, kleptoparasitism was less frequent than when all of the available suet was in clumps as in Regime 4. This was despite the fact that the reward for a kleptoparasite usurping a finder at a clump would have been identical in both regimes. This result is consistent with the idea that personal foraging

Table 2. Correlation between individual foraging intensity variables and measures of kleptoparasitism. N = 16 individuals in all cases, except for the last column where N = 14 (2 birds not known to kleptoparasitise).

	Percentage of kleptoparasitic opportunities acted upon		Mean finder's advantage per kleptoparasitic opportunity		Mean usurper's reward per kleptoparasitic opportunity	
	r	P	r	P	R	P
3 s median inter-toss time	0.02	0.95	0.13	0.37	0.02	0.95
6 s mean inter-toss time	0.15	0.58	0.06	0.81	−0.08	0.79

Table 3. Results of paired t tests comparing a bird's transformed inter-toss intervals when subordinate or when dominant in a group of 2 with the same bird's ITI's when alone. The first two table columns give the food regime, a visual description of the relative amount of kleptoparasitic opportunity afforded by that regime. d1 is the mean (across all birds) of the difference between the transformed inter-toss intervals measure when subordinate to another bird and when feeding alone, SE, the standard error on this value, t is the t-value of a t test comparing the mean with zero, N1 is the number of birds and P is the probability associated with the t-test. Birds were only included in this analysis if they had at least 3 records from both suet regimes. Negative values of d1 and d2 indicate mean inter-toss intervals were lower when birds were in groups of two, compared to when they were solitary.

Regime	Kleptoparasitic opportunity	Subordinate vs Solitaire					Dominants vs Solitaires				
		d1	SE	t	N1	P	d2	SE	t	N2	P
3 s median											
1	+	−1.30	0.61	−2.21	13	0.047	−1.46	0.67	−2.48	11	0.034
2	0	−1.91	0.56	−3.32	13	0.006	−1.17	0.99	−1.20	11	0.26
3	+	−1.94	0.83	−2.42	11	0.043	−4.25	0.49	−2.54	11	0.013
4	+ +	0.02	1.27	0.02	11	0.99	−1.56	0.85	−1.83	11	0.10
5	+ + −	−1.56	0.70	−2.22	9	0.06	−0.72	0.46	−1.59	10	0.15
6 s mean											
1	+	−4.00	1.05	−3.81	13	0.002	−3.75	1.05	−3.57	13	0.004
2	0	−3.84	0.84	−4.54	13	0.001	−3.61	0.75	−4.80	11	0.001
3	+	−5.73	1.54	−3.71	11	0.004	−5.09	1.23	−4.14	11	0.002
4	+ +	−1.21	1.11	−1.09	11	0.31	−3.83	1.50	−2.31	11	0.043
5	+ + −	−3.81	0.83	−4.60	9	0.002	−2.23	0.76	−2.92	10	0.017

and detecting kleptoparasitic opportunities may be partly incompatible: potential kleptoparasites may have paid less attention to others when they could regularly find food themselves, and hence identified fewer kleptoparasitic opportunities. Alternatively, they may have identified but ignored these opportunities because of their own foraging success. Alternatively or additionally, the costs of making a mistake may reduce the benefits of kleptoparasitism in this case: dominants must wait to decide whether the subordinate has found one suet shred or a clump, since erroneous usurpations may cost the dominant in terms of their own foraging time and in depriving them of further opportunity to exploit that subordinate. However, if this "indecision" were occurring we would expect to see a higher finder's reward in this regime, something not shown by our data.

We now turn to our main consideration, the possibility of a trade-off between being observant for opportunities to kleptoparasitise and searching for food. Although kleptoparasitism did occur frequently, the possibility of kleptoparasitising suet did not appear to influence a dominant's personal searching rate. In contrast to expectations of a reduction in personal foraging effort when kleptoparasitic opportunities were present, effort always increased when a bird foraged with a subordinate conspecific (as evidenced by a lower average inter-toss time). This may be related to a reduction in anti-predatory vigilance due to increased protection from predation in a group of two (Pulliam 1973, Elgar 1989). Even with this potential confounding effect, we might still expect the group-size effect to be greatest (i.e. the increase in personal foraging effort as evidenced by reduction in inter-toss times to be greatest) when there were no kleptoparasitic opportunities. However, there was little evidence that the magnitude of the possible group-size effect was dependent on the availability of kleptoparasitic.

There was no evidence that kleptoparasitism was more frequent amongst individuals that had lower personal foraging speeds, suggesting that a bird's personal foraging effort is largely adjusted in relation to perceived risk of predation or perhaps conflict with other blackbirds (see Cresswell 1997) rather than to kleptoparasitic opportunities. Nevertheless there was an increase in the rate of kleptoparasitism when the rewards of kleptoparasitism were higher. This suggests that detection of kleptoparasitism opportunities does not conflict with personal foraging effort within our system. Birds can certainly detect predators with their heads down (Cresswell 1994, Hilton et al. 1999) and one species at least also have ramp retinas (Martin 1986) which allow them to focus on near as well as far objects simultaneously. It is also clear that birds that are not scanning can respond to some behaviours by neighbours (Cresswell et al. 2000). Therefore, it is entirely possible that scanning for kleptoparasitism information is reasonably compatible with foraging. The system we used was one where blackbirds could view other birds as they lifted their heads to toss over leaves or to swallow, but viewing during feeding would certainly be interrupted. Also our system was relatively simple because a dominant only had to keep an eye on a single neighbour. Nevertheless our study presents the first empirical data to suggest that, in contrast to the assumptions of several theoretical works (e.g. Broom and Ruxton 1997), there is not an obvious trade off between time spent personal foraging and time spent monitoring others for kleptoparasitism opportunities. Our results are different from the only other empirical test of this trade off. Coolen et al. (2001) studied spice finches (*Lonchura punctulata*) in an aviary. They found that the frequencies with which a bird hopped with its head pointing up and down were statistically associated with kleptoparasitism and food finding respectively. However, their results are not clear cut. In only one of their three experiments did they find negative relations between hopping with the head down and kleptoparasitism, and between hoping with the head-up and food finding. Hence, they find some evidence of a trade-off, but find that it is not universally displayed in their system. We could find no evidence of a trade-off in our system. Taken together, both papers suggest that the hypothesised trade-off can be present but is not universally applicable. The challenge for future work is to delineate circumstances where it does and does not apply.

It is only recently that theory has addressed the idea that kleptoparasitism could be a flexible tactic, with its use being influenced by ecological conditions. Stillman et al. (1997), Broom and Ruxton (1997) and Sirot (2000) all predicted that aggressiveness should increase when food patches are harder to find and when their value increases. These predictions find support from our data. The theories differ in that Stillman et al. and Broom and Ruxton predict a step change in behaviour, with individuals either always or never attempting kleptoparasitism, whereas Sirot predicts that individuals should adopt mixed strategies, only acting on a fraction of the kleptoparasitic opportunities that present themselves. Our data appear more consistent with the prediction of Sirot. However further experiments where food availability was subject to greater variation would provide a critical test between the predictions of these two theories.

The most detailed theoretical description of kleptoparasitism is given by Stillman et al. (1997). They suggest that kleptoparasitism should be flexible, with aggression only occurring when the benefits of this action outweigh the costs, a prediction that finds support in our work. They also predict that the potential victims of kleptoparasitism modify their positioning, their diet choice and/or their food handling methods so as to reduce the risk of kleptoparasitism. These predictions have yet to be explored empirically. However, the study system presented here would seem an ideal test bed for such study.

Acknowledgements – We thank Paul Normand, Tom Weaver, the Marquis of Linlithgow and all at Hopetoun House for practical help. Our work was carried out under a NERC research grant to Graeme Ruxton and Will Cresswell. This paper was greatly improved by the perceptive comments of two referees.

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OIKOS 97: 213–222, 2002

Fitness consequences of the timing of metamorphosis in a freshwater crustacean

Sarah Twombly and Nancy Tisch

Twombly, S. and Tisch, N. 2002. Fitness consequences of the timing of metamorphosis in a freshwater crustacean. – Oikos 97: 213–222.

Metamorphosis is a common life-cycle transition in organisms as diverse as amphibians, insects, fishes and crustaceans, and the timing of this transition often affects an individual's fitness. Here, we measured age and size at metamorphosis in laboratory-reared individuals of the freshwater copepod, *Diaptomus leptopus*, and then followed individuals over their entire life cycle to assess the fitness consequences of variation in age and size at metamorphosis. In 3 separate experiments, individuals were raised in different food conditions: low food (0.2 μg C/ml) switched to high food (0.7 μg C/ml), or high food switched to low food, at several different larval and juvenile stages. Control individuals were reared on high or low food concentrations over their entire life cycles. For each individual, we measured age and size at metamorphosis and age and size at maturity; for females, we also measured total lifetime egg production, longevity, and calculated a composite fitness measure, λ. Statistical analyses showed no significant effects of age or size at metamorphosis on these same traits measured at maturity, or on the fitness components we estimated. The first individuals to mature had the highest total egg production and individual fitness; differences in body size at maturation explained none of the variation observed in fitness components. Our results show that metamorphosis was decoupled from maturity and from fitness components by growth and development achieved during the juvenile phase of the life cycle, and support the conclusion that fitness consequences of metamorphosis depend fundamentally on the organization of an organism's life cycle. They also suggest that body size plays a different life history role in these organisms than is recognized in most poikilotherms, and suggest the hypothesis, based on laboratory experiments, that selection may act primarily on juvenile developmental rates in field populations.

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Complex life cycles are characterized by an abrupt ontogenetic change in an individual's morphology, physiology, behavior and ecology that is defined as metamorphosis (Wilbur 1980). This transition is common among diverse organisms ranging from amphibians and insects to fish and crustaceans. Within any of these taxa, the age and size at which metamorphosis occurs vary among individuals (Wilbur and Collins 1973, Semlitsch and Gibbons 1985, Chambers and Leggett 1987, Forrest 1987, Newman 1992, Twombly 1995). Because the timing of metamorphosis is often assumed to affect an individual's fitness, variation in these traits has attracted considerable theoretical and experimental interest (Alford and Harris 1988, Hensley 1993, Leips and Travis 1994, Bradshaw and Johnson 1995, Hentschel 1999, Morey and Reznick 2000).

Age and size at metamorphosis often affect components of fitness directly. For example, these traits influence age and size at maturity in several amphibians (Berven and Gill 1983, Smith 1987, Semlitsch et al. 1988, Scott and Werner 1990) and insects (Moeur and Istock 1980, Blakley 1981, Hard et al. 1989). Female

Accepted 6 November 2001

ISSN 0030-1299

