

Short Communications

Social Foraging in Cliff Swallows: a Critique

Many animals forage in groups either to reduce predation hazard, to obtain foraging benefits, or both (Clark & Mangel 1986). Recent theoretical models have suggested that local enhancement, the use of others' foraging activities as cues to find food, can reduce the variance in an individual's foraging success (Caraco 1981). Although this prediction has been tested with groups of captive animals (Baker et al. 1981; Theimer 1987; Ekman & Hake 1988), field evidence of the use of foraging groups as a risk-averse strategy is rare (Uetz 1988). Therefore, field data on local enhancement and risk sensitivity would be extremely valuable and influential. In this context, Brown's (1988) data set on cliff swallows, *Hirundo pyrrhonota*, is impressive both for its volume and for its field approach. Despite this, the study makes several claims that are not entirely supported by the data. In particular, the study concludes that: (1) cliff swallows use local enhancement, (2) predator avoidance plays a minor role in swallow group foraging, (3) there is little evidence for competition within swallow foraging groups, and (4) the data provide the first empirical demonstration of simultaneous risk-aversion and risk-proneness in a free-living population of animals. In the following discussion, we question these conclusions and suggest what type of data would be required to support them.

Brown's evidence that cliff swallows use local enhancement is essentially the instantaneous convergence of animals at the same foraging site (page 784). This cannot be considered sufficient evidence for local enhancement, however, because such convergences are to be expected in species whose resources are clumped. Individuals could be responding to the resource itself or to stimuli other than foraging individuals. Although the descriptions of swallows apparently observing the foraging behaviour of others are suggestive, they cannot be argued to provide evidence of local enhancement. Showing that swallows arrive more quickly in patches that are being exploited by others than in equivalent patches that have not yet been discovered would be more convincing evidence of this phenomenon (Waite 1981).

Brown concludes that predator avoidance plays a minor role in a cliff swallow's decision to forage in a group because of a lack of higher vigilance levels in birds on the flock periphery and the absence of a tendency for individuals to prefer central flock positions. The lack of higher vigilance at the per-

iphery of flocks is based not on a direct measurement of vigilance but on foraging rate. Thus, he assumes that foraging and vigilance are incompatible activities. Such an assumption is commonly made in studies of vigilance patterns in ground feeding birds and this is acceptable when, for instance, looking for food on the ground excludes watching for aerial predators (Pulliam et al. 1982). It is not obvious, however, that this assumption can also be applied to the novel context of aerial foragers watching for aerial predators. Without justifying the use of this assumption, the similarity in the foraging rates of central and peripheral birds cannot provide evidence that predation is unimportant to swallows. Even if foraging and vigilance were incompatible activities, aerial foraging in a flock could present special circumstances where different vigilance levels would not be expected. For instance, it is possible that in aerial foraging flocks central birds need to invest extra vigilance simply to avoid colliding with other foragers. Risk of collisions can have a significant influence on individual foraging decisions (Guilford & Cuthill, unpublished data), and could also explain Brown's observation that swallows do not favour central flock positions. More powerful evidence that predation hazard is not important for flock foraging swallows would require observations that swallows do not behave in the ways predicted by the anti-predation hypotheses when in the presence of predators (Caraco et al. 1980).

Brown concludes that there is little evidence for competition or resource depression in swallow flocks, 'assuming that such competition would result in lowered feeding rates in the large groups' (page 790). There is no basis for this assumption since competition in ideal free animals is expected to lead to equal foraging gains in different-sized foraging groups (Fretwell & Lucas 1969). Competition, therefore, may indeed have been at work shaping group size to local food abundances. Brown also suggests that competition is weak due to the ephemerality of the food patches. He states that patches rarely last more than 10–15 min, although duration appears quite variable, ranging from 5–30 min (page 784) to 4–5 h (page 785). To demonstrate patch ephemerality, however, one would need to show that the duration of a food patch is independent of the size of the group exploiting it. This information is lacking and the data do not therefore provide evidence for the absence of food competition within foraging groups.

The most important contribution of Brown's study is the clear evidence that variance in capture attempts per minute (foraging success) decreases as group size increases. These data are consistent with risk-sensitive models as Brown argues, and, inasmuch as these models assume that group foraging reduces the variance of foraging success, we agree. However, he also says that 'there are no previous data that demonstrate the simultaneous occurrence of risk-prone and risk-averse foraging strategies in natural populations of free-living animals' (page 789). Such a demonstration would require data showing that animals respond to variance in foraging success. The study provides no evidence of this. In fact, the data indicate that solitary individuals whose foraging success is lower than that expected in a group join groups, whereas solitary individuals whose mean foraging success is greater than that expected in a group continue to forage alone (Table IB, Brown 1988). These data suggest that the decision of solitary swallows is based on the mean rate of prey capture attempts and not on the variance. If solitary animals are in fact risk-prone, that is, in poor condition and unlikely to achieve a sufficiently high rate of prey encounter to avoid starvation, then poor performance when alone should increase risk-proneness and a tendency to remain alone. This is exactly the opposite of what Brown reports. To provide an empirical demonstration of risk-proneness and risk-aversion, it must be shown that the swallows respond to the variance in capture attempts, not to the mean, and that the birds that choose to forage solitarily are those in the worst condition. Mere presence in a flock or solitary foraging cannot simply be equated with risk-aversion or risk-proneness, respectively (Caraco 1981).

Field studies are admittedly difficult to conduct and the problems with Brown's study are by no means unique. However, we feel that if these studies are to be effective tests of social foraging hypotheses, it is necessary to urge a more critical approach when confronting field observations with theoretical predictions.

We thank Don Kramer, Jim Grant, Jim Mountjoy, Bill Vickery, Patrick Colgan, Ian Jamieson and the Inter-university Social Foraging Discussion Group for comments. Financial support was provided by an NSERC postgraduate scholarship to J.J.T. and an NSERC University Research Fellowship and Operating Grant to L.-A.G.

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(Received 12 January 1989;
initial acceptance 21 February 1989;
final approval 24 April 1989;
MS. number: AS-604)

Are Cliff Swallows Risk-sensitive, or Mean-rate Maximizing?

Brown (1988) recently interpreted his data on cliff swallows, *Hirundo pyrrhonota*, as the first demonstration of both risk-prone and risk-averse foraging in a population of free-living animals. Cliff swallows may be risk-sensitive, but, in building the case for this conclusion, Brown does not consider and reject the equally plausible alternative that the birds are simply maximizing the long-term average rate of prey harvest (mean-rate maximizing). Until that is done, readers should remain sceptical.

A risk-prone forager is one that prefers a probability distribution of rewards to the distribution's mean value with certainty. A risk-averse forager