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Viable and unviable hypotheses for the evolution of raven roosts

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Recently, Marzluff et al. (1996) 'tested the central requirement of the information centre hypothesis . . . that naïve members of a roost follow knowledgeable members to newly discovered foods'. Their experiments show that information on food location is transferred from knowledgeable birds to birds lacking such information. Experiments of this kind are rare and the data presented are indeed outstanding. Here we argue that this 'central requirement' is also predicted by two alternative hypotheses, or even by simple information parasitism. Moreover, the information centre hypothesis (ICH), as proposed by Ward & Zahavi (1973), is based on reciprocity, which is highly unlikely in large communal roosts, and in particular, in raven roosts with unstable membership, as also pointed out by Marzluff et al. (1996). We suggest that the data should not be interpreted as supporting the ICH. In our opinion, most results presented by Marzluff et al. (1996) fit the predictions of the recruitment centre hypothesis (RCH; Richner & Heeb 1995, 1996) instead.

The core of the information centre hypothesis is Ward & Zahavi's (1973) proposition that communal roosting or breeding evolved through the benefits arising from information transfer at the roost: a forager that is unsuccessful on one occasion can follow a successful forager when leaving the communal site, and will in turn, be followed on the occasions when it has foraged successfully. Thus, the ICH is meant to provide an ultimate, functional explanation for the evolution of communal behaviour based on a mechanism that requires a stringent form of reciprocity (i.e. reciprocal altruism sensu Trivers 1971). An individual that has found a food source will return and lead birds from the communal site to the source. Leading others to the source and sharing food entail a

cost $|x|$. However, on a subsequent occasion, this individual may be in the role of being led to a food source and thereby enjoy a benefit $|y|$. Thus, for an individual that has been at least once in both roles, the net benefit would be $|y| - |x|$. A net benefit arises as long as the benefit of following $|y|$ is greater than the cost of leading $|x|$ (see Fig. 1).

Despite hundreds of studies published on the ICH, compelling evidence for the ICH is lacking (for reviews see Mock et al. 1988; Richner & Marclay 1991; Richner & Heeb 1995; Danchin & Wagner 1997). This is no surprise given the stringent conditions for reciprocal altruism that (1) the cost of giving information is small compared to the benefits of receiving information, (2) individuals that give information to an individual on one occasion are likely to receive information from this individual on a subsequent occasion, and (3) nonreciprocators can be identified and excluded (Trivers 1971, 1985). These conditions are unlikely to be fulfilled in large assemblages and have never been tested in any of the published studies on the ICH. High mobility of individuals, as is typical for roosts, further limits the potential for co-operation (Enquist & Leimar 1993; Houston 1993), and thus greatly reduces the potential for a roost to function as an information centre based on reciprocal altruism. Without reciprocal altruism, the ICH is unviable because an ICH-based assemblage could easily be invaded by behavioural mutants, which only return to the communal site when looking for a source of food, but not when they discover food themselves. At the very least, this may lead to a frequency-dependent equilibrium between reciprocators and nonreciprocators. Obviously, an existing roost or breeding colony is open to information parasitism as long as some benefits arising from communal roosting or breeding outweigh the cost of information parasitism. Such an assembly will, seen superficially, show a number of features predicted by the ICH. Information transfer per se, however, is in this case a by-product of selection for communal living arising

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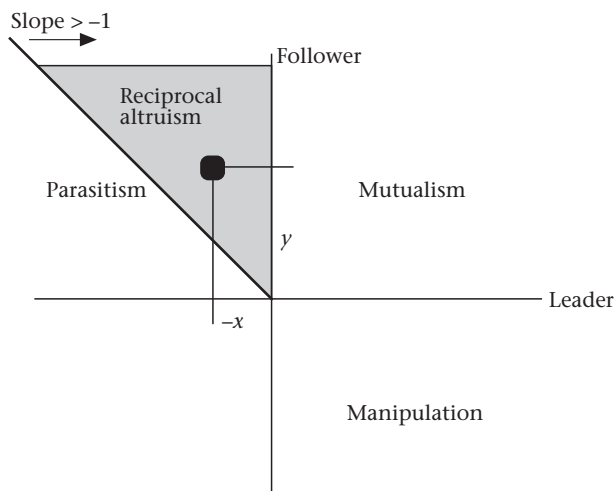


Figure 1. Mechanism underlying the information centre hypothesis. Axes represent the costs (negative values) and benefits (positive values) of information parasitism in the followers (Y axis) and the leaders (X axis). An individual, A, locates a food source and returns to the communal site. In the role of a leader, it guides the colony or roostmates to its newly discovered feeding site. For A, returning and food sharing entail a cost $|x|$. Subsequently, individual A, now in the role of a follower, is led to a food source discovered by individual B and enjoys a benefit $|y|$. The net benefit for A is $|y| - |x|$. It is positive within the shaded area (i.e. for values of $|y| > |x|$). This corresponds to what Trivers (1971, 1985) called reciprocal altruism. In this area, in a given event, the follower parasitizes the information of the leader, but individuals that give information to an individual on one occasion are likely to receive information from this individual on a subsequent occasion. This supposes that nonreciprocators can be identified and excluded.

through other benefits, but not the cause for the evolution of such a life-style. Communal living may include both communal roosting and communal breeding and their evolution can conceptually be based on similar pathways. Information parasitism though is much more likely to occur at breeding colonies because birds are obliged to return to feed their dependent offspring.

Several hypotheses have been proposed to account for communal roosting or breeding that do not require reciprocity (Danchin & Wagner 1997). Such hypotheses may involve habitat selection ('traditional aggregation hypotheses': Shields et al. 1988; Brown et al. 1990; 'performance-based conspecific attraction hypothesis': Monnat et al. 1990; Danchin et al. 1991; Zicus & Hennes 1991; Reed & Oring 1992; Cadiou et al. 1994; Boulinier & Danchin 1997; Danchin et al. 1998), sexual selection ('hidden lek hypothesis': Møller 1987; Wagner 1993, 1997; Post 1994; Hoi & Hoi-Leitner 1997) or improved food finding ('two-strategies hypothesis': Weatherhead 1983; 'recruitment centre hypothesis': Richner & Heeb 1996). They all involve information gathering or information transfer at the communal site.

The two hypotheses that are explicitly related to food finding are based on a direct benefit arising to the individual that gives information concerning food location to other individuals. In the 'two-strategies hypothesis' (TSH) (Weatherhead 1983), strategist A,

characterized by having an above-average efficiency in finding rich food sources, gives food location information to strategist(s) B upon returning to a roosting or breeding site that is buffered by strategist(s) B and therefore above average in terms of its safety from predation. Strategist(s) B experience higher risk at the roost but benefit from following strategist(s) A to their rich food source(s). Thus, a net benefit accrues to strategist A at the communal roosting or breeding site, and to strategist B at the feeding site.

In the recruitment centre hypothesis (RCH) (Richner & Heeb 1996), benefits arise to both the leader and the follower at the feeding site. It proposes that an individual that has successfully located a food patch will return to the communal site to recruit foragers because of the benefits arising from group foraging. These benefits must outweigh the summed costs of returning to the communal site and giving away food location information. Many studies have documented beneficial effects of group foraging, either through a higher feeding rate or a lower predation rate (e.g. Caraco 1979; Barnard 1980; Elgar & Catterall 1981; Pitcher et al. 1982; Lendrem 1984; Pulliam & Caraco 1984). Using Zahavi's (1975, 1977, 1987) 'honesty-by-cost' principle, the recruitment centre hypothesis can also account for the aerial displays and calling observed at roosts. Aerial displays can be costly (Hails 1979; Møller 1991; Mather & Robertson 1992), and the successful forager that derives the highest net benefit by increasing feeding group size through escalated aerial displays will be the most willing to engage in them. The recruitment centre hypothesis makes a number of predictions (Table 1), primarily with regard to feeding and displays: (1) the net benefit to a forager at a food patch is greater after returning and feeding with recruits than when it previously fed without recruits; (2) the payoffs of the two strategies should be frequency dependent, that is, form an evolutionarily stable strategy (ESS) (Richner & Heeb 1995; Barta & Szép 1992), and searching for food or waiting to be recruited at a roost should therefore provide equal net benefits; (3) foragers with relatively higher expected net benefits arising from the increase in foraging group size will show relatively more escalated aerial or vocal displays; (4) recruiting activities and displays should be most intense immediately after the discovery of a new food patch, and then level off; (5) birds will stop recruiting other birds at the communal site when no additional benefit can be achieved by a further increase in feeding group size; and (6) foragers that are already feeding in a group of the optimal size should remain silent at the colony. This could also explain why some successful foragers advertise and others do not, as has been reported in a study on the black-billed gull, *Larus bulleri* (Evans 1982).

Marzluff et al. (1996) claim that their observations and experiments show that raven roosts function as information centres and thus supposedly support Ward & Zahavi's (1973) information centre hypothesis. Evidence for reciprocation, which would be a prerequisite for supporting the ICH, is lacking, and as Marzluff et al. (1996) point out, the instability in the membership of feeding and roosting groups of ravens reduces the potential for

Table 1. Predictions and requirements of the information centre hypothesis (ICH), the two-strategies hypothesis (TSH) and the recruitment centre hypothesis (RCH)

	ICH	TSH	RCH
Reciprocity	Mandatory	Not required	Not required
Type of benefit	Reciprocal	Mutual	Mutual
Currency of benefit	Food	For some phenotypes food, for others safety from predation	Food (and safety from predators)
Variation of net benefit among individuals	Variation possible	Variation possible	No variation, equal benefits maintained by frequency dependence
Range of phenotypes at communal site	All individuals are equally efficient at locating food sources in order to ensure reciprocity	Some individuals are more efficient at locating food sources than others	Individual variation in locating efficiency can exist but is not required
Feeding success of discoverer when returning from communal site with co-feeders to food patch	Decreases	Decreases	Increases
and/or			
Predation risk after returning to food patch	No prediction by original hypothesis	No prediction by original hypothesis	Decreases
Stability in the membership of feeding and roosting groups	Required	Not required	Not required
Function of display at communal site	(1) Indication of roost position (Ward & Zahavi 1973) (2) Indicates the 'mood' of the roost (Ward & Zahavi 1973); i.e. the amount of feeding site information available in the roost (3) Assessment of competitive strength at a food patch (Zahavi 1986)	Advertisement of social status to secure access to a safe roosting site	Recruitment of co-feeders
Timing of display at communal site	Displays should be weak after discovery and may then increase	No specific prediction with regard to timing	Displays peak right after discovery and then decline
Group-size related dynamics of display at communal site	Displays should increase with increasing foraging group size (e.g. when more competitors are present, more information is available)	No group-size related displays predicted	Displays decrease with increasing foraging group size

reciprocity to favour information transfer. In the RCH, in contrast, there is no need of reciprocity because the benefits of sharing information are immediate, through the positive effects of group foraging. Thus, a recruitment centre can also develop in a system with high instability of group membership. Marzluff et al. (1996) have further shown that raven roosts are comprised of both knowledgeable and naïve individuals, and that departures from the roosts are highly synchronized. Experiments showed that birds made naïve of the location of food sources followed roostmates to new feeding sites. Birds made knowledgeable of the location of food sources, by being released at new carcasses, joined roosts and led roostmates to food on three of 20 occasions. Thus, some information is exchanged at the communal site, with knowledgeable individuals leading their roostmates to recently discovered food sources. This may involve specific displays at the roost such as social soaring and honking. Social soaring at roosts is the main display at the communal site, and 'individual ravens were attracted from a distance of at least 10 km to those that were soaring' (Marzluff et al. 1996). Social soaring peaked right after the discovery of a new food source, and declined in frequency as feeding group size increased. At dawn, prior to synchronous departure from the roost, a few ravens initiate conspicuous 'honking' vocalizations building to a crescendo. Marzluff et al. (1996) mention that it is unknown whether knowledgeable birds may honk or be silent. According to the RCH, ravens should honk when attempting to increase foraging group size, but remain silent if no further benefit arises from an increase in feeding group size. A recruitment strategy from roosts is most likely to occur when the benefits arising from group feeding are high, and when the likelihood of independent discovery of food or local enhancement is low, as is typical for ephemeral food sources. Raven roosts are mainly comprised of vagrant nonbreeders, which feed on patchily distributed and ephemeral food sources and need information on current food dispersion (Marzluff et al. 1996). At the food source they must compete with the dominant territory holders (Heinrich 1988). They 'are subordinate to local territory holders and have difficulty foraging at defended foods until a group is assembled' (Marzluff et al. 1996, page 100). Thus, a large number of observations are in agreement with the predictions from the RCH, but in disagreement with the ICH (Table 1).

In summary, the finding that (1) in ravens reciprocal altruism is unlikely, (2) members of raven roosts can derive large benefits through group foraging by recruiting roost members at a feeding site, (3) the timing of displays is correlated with food discovery and therefore feeding group size, and (4) specific displays (social soaring and honking) act as recruitment displays at the roost, suggest that raven roosts function as centres for recruitment of co-feeders. We insist on the necessity for testing the assumptions and predictions that allow us to differentiate between different hypotheses (see Table 1). The outstanding results by Marzluff et al. (1996) suggest that roosting ravens may be an excellent model species to test these specific predictions. We suggest further that the information centre hypothesis should not be used for explaining

the evolution of colonial behaviour unless reciprocity *sensu* Trivers (1971, 1985) has been convincingly demonstrated. Because such reciprocity is unlikely to occur in many roosting groups, we believe that the recruitment centre hypothesis is both a more parsimonious and more likely, although not exclusive, explanation for the evolution and/or maintenance of communal roosting. However, the use of a modelling approach is badly needed to clarify the debate about the role of improved food finding in the evolution of communal roosting or breeding in relation to other recent hypotheses (Danchin & Wagner 1997). Such models should be designed to first test the evolutionary stability of the strategies underlying the different hypotheses, and second, test the capacity of each such strategy to generate animal aggregation and patterns similar to coloniality.

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