



## FORUM

## On the importance of slight nuances in evolutionary scenario

H. RICHNER\* &amp; E. DANCHIN†

\*University of Bern

†Zoology Department, Université Pierre et Marie Curie

(Received 23 November 1999; initial acceptance 16 June 2000;  
final acceptance 10 September 2000; MS. number: AF-8)

The aim of our original comment to Marzluff et al.'s (1996) paper was to reveal some of the problems with their claim that the data show that raven roosts function as information centres sensu Ward & Zahavi's (1973) information centre hypothesis (ICH). We also pointed out that their findings are compatible with the predictions from the recruitment centre hypothesis (RCH; Richner & Heeb 1995, 1996) and a few other hypotheses, which in itself, is sufficient for not accepting their claim. In their reply, Marzluff & Heinrich (2001) make three main points.

First, Marzluff & Heinrich (2001) use a stark misrepresentation of the Ward & Zahavi (1973) paper. Ward & Zahavi (1973, page 532) make clear that the ICH is a functional and thus ultimate evolutionary explanation of communal behaviour by stating 'evidence is presented to support the hypothesis that communal roosts, breeding colonies and certain other bird assemblages have been evolved primarily (emphasis ours) for the efficient exploitation of unevenly distributed food sources by serving as information centres'. Returning of a successful forager to the roost 'is seen as a form of insurance against the occasional risk of losing a hitherto good feeding place' (Ward & Zahavi 1973, page 517). Thus Ward & Zahavi framed an evolutionary scenario and postulated a precise mechanism for the formation of bird assemblages. Hence, by definition, the information centre hypothesis deals with the evolution of communal behaviour, and should not be applied to the simple observation of information transfer at the communal site.

Second, Marzluff & Heinrich's (2001) claim that the purpose of their original paper 'was not to investigate the evolution of communal roosting, but to test whether nocturnal roosts of ravens function as information

centres...'. However, in their original paper Marzluff et al. (1996) state (pp. 89–90) that they 'tested a central requirement of the information centre hypothesis', and thereby clearly refer to Ward & Zahavi's (1973) original hypothesis. As pointed out above, the ICH is not a proximate hypothesis simply holding that information is exchanged. Showing that information is transferred does not show the existence of an information centre in the sense of the ICH (Mock et al. 1988; Richner & Heeb 1995). Many other hypotheses, such as the RCH (Richner & Heeb 1995, 1996), the two-strategies hypothesis (Weatherhead 1983), the simple information parasitism hypothesis (Richner & Heeb 1995) and others also predict information exchange at the communal site. If the simple aim of Marzluff et al. (1996) was to show that assemblages allow individuals to get information, then the study should not be presented as support or testing of the ICH. Rather it should be stated that the findings are inconclusive with respect to these various hypotheses.

Third, Marzluff & Heinrich (2001) suggest that 'Danchin & Richner might therefore classify our system as an information centre from the perspective of naïve birds and as a recruitment centre from the perspective of knowledgeable birds'. However, each of the two hypotheses was originally meant to describe the whole system, and it therefore does not make sense to say that one part is ICH and the other part is RCH. They also state 'We do not see the utility of this distinction except as a way to emphasize that all roost members benefit by the open sharing of information we documented'. 'It is particularly inappropriate to develop a new hypothesis (the RCH) to account for a subset of the conditions consistent with the ICH' (emphasis ours). It should be clear that the RCH is not a simple subset of the ICH. The two hypotheses are based on two distinct mechanisms leading to information sharing. They have different assumptions and make different predictions (Table 1 in Danchin & Richner 2001). In the ICH, the roosts and colonies serve as a pool of information on the location of feeding sites and the displays are

Correspondence: H. Richner, Zoology Department, University of Bern, CH-3032 Hinterkappelen-Bern, Switzerland (email: richner@esh.unibe.ch), or E. Danchin, Université Pierre et Marie Curie, Bât A, 7e étage, Case 237, 7 quai Saint Bernard, 75252 Paris Cédex 05, France (email: edanchin@snv.jussieu.fr).

advertisements for the placement of the colony and its 'mood' (Ward & Zahavi 1973). In the RCH, communal sites serve as a pool of potential recruits and the displays are honest signals indicating the quality of the food patch found by the displaying bird. It had been suggested erroneously that the RCH also involves a group selection argument (Zahavi 1996), although it was made clear (Richner & Heeb 1995, 1996) that the recruiting of co-foragers is to the individual benefit of the bird that located a new food patch, arising through the well-documented advantages of group foraging (e.g. Pulliam & Caraco 1984).

More generally, slight nuances in evolutionary scenarios may strongly affect evolutionary stability. The case of the prisoner's dilemma, where two players can either cooperate or defect, provides an excellent example to illustrate the point. It had been first proposed that the evolutionarily stable strategy was 'tit for tat' (TFT: cooperate after a cooperation of the co-player in the previous move, otherwise defect: Axelrod & Hamilton 1981; Axelrod 1984). Since then it has been shown that a population of TFT-strategists can be invaded by 'generous TFT'-strategists (cooperate after a co-player cooperated, but allow occasional defection by the co-player; Nowak & Sigmund 1992). Thus the slight rate of tolerance is a 'slight nuance' in or 'a subset' of the cooperation scenario but makes all the difference as to which strategy will be evolutionarily stable. At the end, only the empirical studies will tell us which strategies animals employ, but without considering the alternatives on theoretical grounds, we may not even be able to recognize the difference. This applies equally well to the various hypotheses explaining enhanced food finding.

From Marzluff & Heinrich's (2001) comments, we suspect that there is a more fundamental difference in approach. Obviously, in a Popperian approach, key scientific advance arises by the accumulation of evidence for or against a hypothesis, by the formulation of alternative hypotheses (often extracted from mathematical models), and by the testing of predictions that allow discrimination between the alternatives. Concerning the ICH, we would like to see theoretical models, based on plausible assumptions, which demonstrate that the ICH is viable without reciprocal altruism, and that cooperation among individuals can operate in large mobile groups of animals (e.g. Houston 1993). Still then, we would need critical tests of predictions not in common with other hypotheses such as the RCH. So far, even if the ICH would turn out to be viable on theoretical grounds, the findings by Marzluff et al. (1996) do support equally well the RCH and other hypotheses. For the evaluation of these alternatives and final progress in the field, we are looking forward to Marzluff & Heinrich's critical further experiments on their ravens.

Since these lines were written, a theoretical paper studying the link between information sharing and

animal aggregation (Lachmann et al. 2000) showed that a key element in this debate is the possibility that animals that discover a food patch may, or may not, be able to hide the information about their feeding success. When the feeding biology of a species is such that individuals cannot hide their feeding success (i.e. the information is nonexcludable, such as in puffins or terns, which return to their nests with fish hanging from their bills), then information sharing is likely to generate aggregation. Thus, we strongly suggest that this important element be taken into account in the debate about information sharing and the evolution of coloniality. In particular, information about feeding success is likely to be easier to hide in roosts than in breeding colonies, implying that information sharing may play a different role in these two situations.

## References

- Axelrod, R. 1984. *The Evolution of Cooperation*. New York: Basic Books.
- Axelrod, R. & Hamilton, W. D. 1981. The evolution of cooperation. *Science*, **211**, 1390–1396.
- Danchin, E. & Richner, H. 2001. Viable and unviable hypotheses for the evolution of raven roosts. *Animal Behaviour*, **61**, F7–F11. <http://www.academicpress.com/anbehav/forum> and <http://www.idealibrary.com>
- Houston, A. I. 1993. Mobility limits cooperation. *Trends in Ecology and Evolution*, **8**, 194–196.
- Lachmann, M., Sella, G. & Jablonka, E. 2000. On advantages of information sharing. *Proceedings of the Royal Society of London, Series B*, **267**, 1287–1293.
- Marzluff, J. M. & Heinrich, B. 2001. Raven roosts are still information centres. *Animal Behaviour*, **61**, F14–F15. <http://www.academicpress.com/anbehav/forum> and <http://www.idealibrary.com>
- Marzluff, J. M., Heinrich, B. & Marzluff, C. S. 1996. Raven roosts are mobile information centres. *Animal Behaviour*, **51**, 89–103.
- Nowak, M. A. & Sigmund, K. 1992. Tit for tat in heterogeneous populations. *Nature*, **355**, 250–253.
- Mock, D. W., Lamey, T. C. & Thompson, D. B. A. 1988. Falsifiability and the information centre hypothesis. *Ornis Scandinavia*, **19**, 231–248.
- Pulliam, H. R. & Caraco, T. 1984. Living in groups: is there an optimal group size? In: *Behavioural Ecology: an Evolutionary Approach*. 2nd edn (Ed. by J. R. Krebs & N. B. Davies), pp. 122–147. Oxford: Blackwell Scientific.
- Richner, H. & Heeb, P. 1995. Is the information centre hypothesis a flop? *Advances in the Study of Behavior*, **24**, 1–46.
- Richner, H. & Heeb, P. 1996. Communal life: honest signalling and the recruitment centre hypothesis. *Behavioral Ecology*, **7**, 115–118.
- Ward, P. & Zahavi, A. 1973. The importance of certain assemblages of birds as 'information centres' for food-finding. *Ibis*, **115**, 517–534.
- Weatherhead, P. 1983. Two principal strategies in avian communal roosts. *American Naturalist*, **121**, 237–243.
- Zahavi, A. 1996. The evolution of communal roosts as information centers and the pitfall of group selection: a rejoinder to Richner and Heeb. *Behavioral Ecology*, **7**, 118–119.