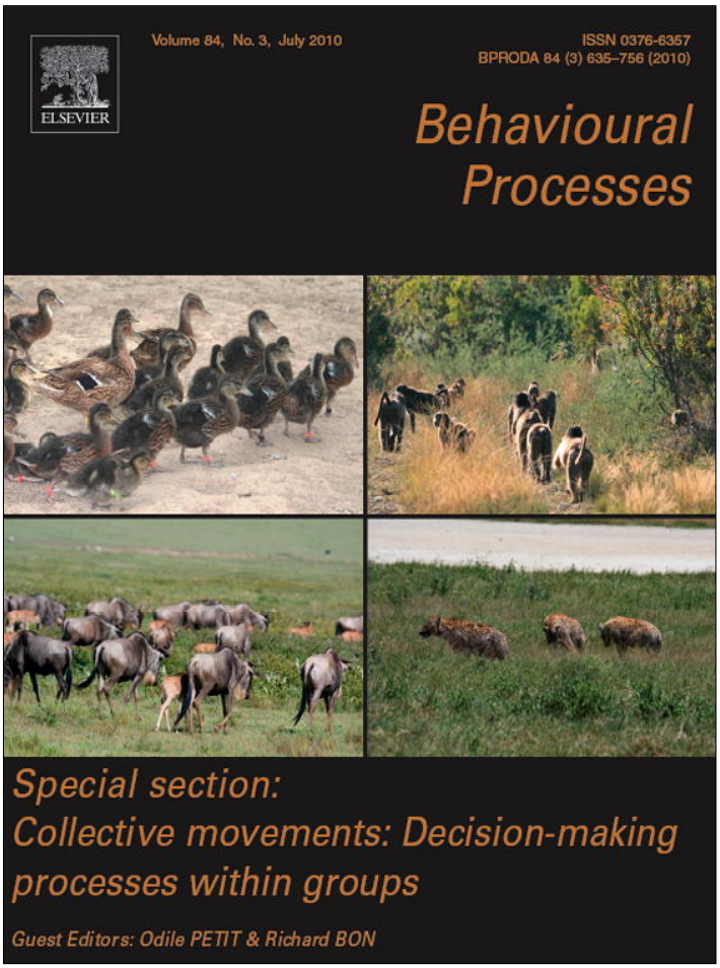

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Commentary

Temporal complementarity of information-based leadership

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In producer–scrounger systems (Barnard and Sibly, 1981), some individuals specialize in finding food while others keep an eye on these producers with a view to share their findings. Conceivably, different individuals living in a group could have different food-finding skills, though all group members would retain the ability to join food discoverers. Thus an individual could be a producer at one time and a scrounger at another. The idea that different foraging specialists within a group could benefit from parasitizing each other's foraging efforts has been called the skill pool hypothesis (Giraldeau, 1984; Giraldeau and Lefebvre, 1986).

A similar concept could be applied to leader and follower roles in those cases where leaders have prior knowledge of where food is likely to be found (the producing skill) and naive followers are capable of sharing that food (the scrounging role). If food availability vary spatio-temporally, it is possible for different individuals at different times to have different knowledge of the location of food. Leader and follower roles could therefore be exchanged from time to time.

The idea that leader and follower roles can be exchanged is at the core of the information centre hypothesis (Ward and Zahavi, 1973), which posits that one of the advantages of communal roosts or breeding colonies in birds is to increase foraging efficiency via the reciprocal exchange of information about ephemeral food locations. For example, crows could forage individually or in small bands during the day, but join a large roost at night. Individuals that foraged unsuccessfully during the previous day could try to follow successful foragers upon leaving the roost the next morning in the hope of joining them at the carcass they have found. Successful foragers could be identified based on their physical condition or the eagerness of their departure flight. There might not be any advantage to the leaders being followed that would sufficiently offset the cost of having to share their food (though one possibility would be the anti-predatory benefits of being part of a group at the feeding site), but if the chances of finding food are more or less uniform across the population, then the leaders of today may still benefit overall from joining the roost because in the near future they may become followers. In a kind of reciprocal altruism, the net benefit for all group members would be to reduce the chance of suffering extended periods without food.

Certain pitfalls have to be borne in mind when testing the information centre hypothesis against other hypotheses that make similar predictions (Bayer, 1982; Evans, 1982; Mock et al., 1988; Danchin and Richner, 2001; Mock, 2001). There is a fair amount of evidence in birds that unsuccessful foragers follow successful ones (De Groot, 1980; Loman and Tamm, 1980; Brown, 1986; Greene, 1987; Rabenold, 1987; Waltz, 1987; Heinrich, 1988, 1994; Marzluff et al., 1996; Sonerud et al., 2001; but see Andersson et al., 1981; and for examples concerning bat roosts, see Wilkinson, 1992; Kerth and Reckardt, 2003). However, there is little if any evidence that one individual switches leader and follower roles depending on its knowledge of food availability (for possible exceptions, see Brown, 1986; Wilkinson, 1992; Marzluff et al., 1996). Intuitively, reciprocal exchange of information seems likely, but it has not been confirmed. Part of the difficulty, at least in the context of bird roosts and colonies, resides in identifying individuals in the field.

Fish shoals represent another system amenable to study in this regard. Naive fish are known to sometimes follow experienced individuals to the site of food or through an escape hole (Warren et al., 1975; Köhler, 1976; Sugita, 1980; Laland and Williams, 1997, 1998; Reebs, 2000, 2001; Swaney et al., 2001; Brown and Laland, 2002; Reader et al., 2003; Dyer et al., 2009). Shoal composition can be fluid in nature (Helfman, 1984), which means that at any one time different individuals may have different knowledge about where and when food is available. Leadership based on information could therefore change from day to day, or even within the same day. However, I am not aware of any field data reporting switches between leader and follower roles according to information status in moving fish shoals. Here, the difficulty resides not only in identifying individuals, but also in observing fish shoal movements under natural conditions.

In a set of preliminary experiments, I have taken these questions to the laboratory. I work with the golden shiner, *Notemigonus crysoleucas*, a gregarious cyprinid that roams widely within lakes (Hall et al., 1979) in shoals of 8–250 individuals (Krause et al., 1996). In a large tank (1.2 m × 1.8 m, or approximately 15 × 23 fish

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lengths), these fish can be trained to associate a particular time of day with a particular corner to obtain food. The movements of shoals of marked shiners can be videotaped with or without prior food training. Some individuals have an intrinsic tendency to be found in front positions (while others tend to stay at the back) during shoal movements, as revealed by observations of shoals made up of fish of similar size and knowledge (Leblond and Reebs, 2006). But if the shoals are made up of a mixture of trained and naïve individuals, then the trained individuals are always in front and they lead the naïve fish to food in the right corner at the right time of day (Reebs, 2000, 2001). When body size differs within a shoal, smaller trained fish lead more often than larger trained fish, possibly owing to a greater need to get food (Reebs, 2001).

Golden shiners are capable of learning to associate different times of day with different locations to get food (Reebs, 1996). It is therefore possible (though still unconfirmed in nature) that fusing shoals could end up having individuals that know about food in one location in the morning and other fish that know about food at another location in the afternoon. Such a shoal could be led to food by one subgroup of leaders in the morning and by another subgroup in the afternoon, resulting in a temporal complementarity of leadership.

I have tested this possibility by training some fish to find food in one corner of the tank in the morning (the "morning corner"), and other fish to find food in another corner in the afternoon (the "afternoon corner"), and then combining all these individuals into one shoal, with or without the addition of naïve individuals. In six preliminary trials (three trials with six morning-trained and six afternoon-trained fish, and three trials with three morning-trained, three afternoon-trained, and six naïve fish), there were always more fish in the morning corner during the morning, and more fish in the afternoon corner during the afternoon, consistent with the idea of temporally complementary leadership. However, shoals often split, and there were often a few individuals in the afternoon corner during the morning, or in the morning corner during the afternoon. In other words, the results were not as clear cut as one might have liked. This experimental paradigm would benefit from some tweaking to make sampling of the wrong corner, as well as shoal splitting, more costly. The introduction of some kind of predatory risk may be indicated.

It is worth pointing out that the notion of temporal complementarity in leadership makes sense only when leadership is based on information. The word "complementarity" implies some advantage to switching leader and follower roles, and it is difficult to find such advantage when leading is based on hunger, exploratory impulse, or intrinsic activity levels (Rands et al., 2003). For example, fish and other animals may occupy leadership positions more often when hungry (Krause et al., 1992, 2000; Krause, 1993, 1994) and so leader and follower roles may alternate as the animals switch between being hungry and satiated (Krause, 1993; Krause et al., 2000), but there is no functional benefit to the animals in the alternation per se. In fact, the notion of complementarity makes sense only when specific benefits can be assigned not only to the leaders (for example, wanting to get to a known source of food) but also to the followers (for example, parasitizing the leader's knowledge). Thus the application of the skill pool hypothesis and information center hypothesis to the study of leadership teaches us to pay attention not only to the motivation of the leaders, but also to that of the followers.

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