Animal Behaviour 106 (2015) 107–114

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Prospecting precedes dispersal and increases survival chances in cooperatively breeding cichlids

Arne Jungwirth*, Jonas Walker, Michael Taborsky

Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Hinterkappelen, Switzerland

ARTICLE INFO

Article history:
Received 12 December 2014
Initial acceptance 11 February 2015
Final acceptance 21 April 2015
Available online 14 June 2015
MS. number: 14-01012R

Keywords:
cichlid
cooperation
fitness effects
informed dispersal
life history decisions
Neolamprologus pulcher
social evolution

When and where to disperse is a major life history decision with crucial fitness consequences. Before dispersing, individuals may benefit from checking the suitability of potential future habitats. In highly social species, such prospecting may be directed towards other groups rather than alternative habitats. This may increase familiarity with neighbours and help individuals to successfully integrate into their group. Previous research on the cooperatively breeding cichlid fish *Neolamprologus pulcher* revealed that individuals frequently engage in between-group prospecting. In this study, a combination of long-term observational data and experimental manipulations in the natural habitat of these fish suggests that prospecting increases survival, improves familiarity with members of neighbouring groups and serves to prepare individuals for between-group dispersal. Our findings highlight that dispersal in cooperative breeders can be a complex process involving interactions of potential dispersers with members of both the current group and groups that are possible targets of dispersal. Members of these groups may have divergent fitness interests regarding decisions of potentially dispersing individuals, which may have selected for the subtle preparation for intergroup dispersal observed in these cooperative cichlids.

Dispersal is an evolving trait and a fundamental feature of life that affects all evolutionary processes from individual fitness to gene flow between populations (Ronce, 2007). Owing to a lack of knowledge about and familiarity with the new environment, dispersal can be a costly enterprise (Bonte et al., 2012). To mitigate this cost, animals may prospect the environment within their potential dispersal range to obtain information about dispersal options (Bocedi, Heinonen, & Travis, 2012; Delgado, Barton, Bonte, & Travis, 2014; Ponchon, Garnier, Grémillet, & Boulinier, 2015). Indeed, dispersal decisions often appear to be informed and based on an evaluation of the current and potential future habitat (Clobert, Le Galliard, Cote, Meylan, & Massot, 2009). In many species, prospecting precedes dispersal and the information gained during prospecting forays influences dispersal decisions (Boulinier, McCoy, Yoccoz, Gasparini, & Tveraa, 2008; Cox & Kesler, 2012; Dittmann, Ezard, & Becker, 2007; Pärt & Doligez, 2003). In highly social animals, the current and future social environment are important determinants of an individual's chances of surviving and reproducing. If reproductive skew within groups is large, dispersal of subordinates may be a means to enhance the chances of gaining direct fitness by joining another group (Cant, Otali, & Mwanguhya, 2001; Clutton-Brock, 1998; Daniels & Walters, 2000; Glander, 1992; Johannesen & Lubin, 1999; Reber, Meunier, & Chapuisat, 2010; Rood, 1987; Sharp, Simeoni, & Hatchwell, 2008).

Between-group dispersal may impose additional costs compared to establishing a new group or territory. First, familiarity among group members is often crucial for the maintenance of cooperation and group stability (Barber & Wright, 2001; Carter & Wilkinson, 2013; McDonald, 2012; Roberts & Sherratt, 1998). Second, dispersal may diminish an individual's relative rank or destabilize the hierarchy in the target group (Dey, Reddon, O'Connor, & Balshine, 2013; Jordan, Wong, & Balshine, 2010; Taborsky & Oliveira, 2012; Wong & Balshine, 2011b). Third, success or failure of a dispersal attempt strongly depends on the respective target group members' behaviour (Stiver, Fitzpatrick, Desjardins, & Balshine, 2006; Taborsky & Oliveira, 2012; Zack & Rabenold, 1989), which may discriminate against a foreign intruder (Hopp, Jablonski, & Brown, 2001; Payne, Payne, Rowley, & Russell, 1991; Radford, 2005; Sturgis & Gordon, 2012). Thus, the success of dispersal in obligate group-living species depends not only on the disperser, but also on the members of potential target groups. In addition, once an individual has left its current group, it may be prohibited from rejoining if dispersal fails. This is because many groups invest communally in a common good, e.g. the

* Correspondence: A. Jungwirth, Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Wohlenstrasse 50a, 3032 Hinterkappelen, Switzerland.
E-mail address: arne.jungwirth@gmx.net (A. Jungwirth).

http://dx.doi.org/10.1016/j.anbehav.2015.05.005
0003-3472/

maintenance of a territory or the storing of food. For such cooperation to be stable, groups have to discriminate against free-riders that try to reap the benefits of the common good without investing in it (Balshine-Earn, Neat, Reid, & Taborsky, 1998; Fischer, Zöttl, Groenewoud, & Taborsky, 2014; Keller & Ross, 1998; Krams, Krama, Igaune, & Mänd, 2007; Lehmann & Perrin, 2002; Smukalla et al., 2008; Strassmann, Gilbert, & Queller, 2011). Future dispersers, however, do not gain from investing in a common good from which they will not benefit in the future (Bergmüller, Heg, & Taborsky, 2005; Zöttl, Chapuis, Freiburghaus, & Taborsky, 2013). Thus, prospective dispersers and individuals that remain in a group face a conflict of interest that probably causes groups to permanently expel individuals that fail to properly cooperate (Cant, 2011; Fischer et al., 2014).

An individual can increase its chances of successful between-group dispersal by familiarizing itself with the target group's members prior to a dispersal attempt. Indeed, individuals in several cooperative species have been described as frequently prospecting foreign groups (Bergmüller, Heg, Peer, & Taborsky, 2005; Doolan & Macdonald, 1996; Kesler & Haig, 2007). This may generate familiarity with members of potential target groups, reduce aggression and thereby enable eventual integration into the respective group's hierarchy. Other potential benefits of such between-group visits have also been proposed, e.g. extragroup matings (Young, Spong, & Clutton-Brock, 2007) or the establishment of safe havens (Bergmüller, Heg, Peer, et al., 2005), besides their potential importance for dispersal (Bergmüller, Heg, Peer, et al., 2005; Cox & Kesler, 2012; Delgado et al., 2014; Doolan & Macdonald, 1996; Kesler & Haig, 2007). Thus, in many cooperative species, individuals appear to build familiarity networks outside their own group by visiting and interacting with foreign groups.

Prospecting itself imposes costs, including an increased risk of predation, opportunity (time) costs and reduced opportunities to help in the home group (Young, Carlson, & Clutton-Brock, 2005). The latter in particular may influence within-group interactions, because prospecting instead of helping may elicit aggression from group members (Balshine-Earn et al., 1998; Fischer et al., 2014). Such aggression may raise the costs of staying in the current group, which can render prospecting and dispersal a more beneficial alternative. This positive feedback may lead to divergent life history strategies, namely staying at home and helping versus dispersing (Bergmüller & Taborsky, 2007; Clobert et al., 2009). Thus, prospecting behaviour can be an important component of group living, within-group cooperation and life history decisions, and hence it constitutes a fundamental feature in the evolution of sociality.

To unravel the long-term consequences of prospecting behaviour, familiarity and dispersal decisions on individual life histories, we studied the obligate cooperative breeder *Neolamprologus pulcher*, a cichlid fish endemic to Lake Tanganyika. In this species, breeding groups defend permanent territories, groups cluster in colonies, individuals frequently make forays to neighbouring groups and dispersal between groups is common (see Methods for a detailed description of the study species). Studying these fish in their natural habitat for 3 consecutive years, we observed how prospecting behaviour relates to individual dispersal decisions and to survival, and how geographical distance, a proxy of the likelihood of previous prospecting, influences familiarity. We hypothesized that forays increase familiarity between individuals from different groups, which should reduce the aggression received in previously visited groups and facilitate successful dispersal into these groups. Thus, we expected individuals performing more prospecting forays to other groups to have higher chances of survival and to be more likely to disperse. In addition, we expected that dispersers would preferentially join groups they had previously visited, and that experimentally opened vacancies would be taken up by fish that had previously made forays to the group in which the vacancy was established. Finally, we expected fish to receive less aggression the closer from home they were intruding into foreign territories. Such results would highlight the importance of prospecting behaviour in establishing relations between individuals from different social units and in preparing for between-group dispersal in highly social animals.

METHODS

Study Site

Using self-contained underwater breathing apparatus (SCUBA), we studied a wild population of *N. pulcher* at the southern tip of Lake Tanganyika, East Africa, off the Zambian coast at Kasakalawe Point near Mpulungu (8°46.849′S, 31°04.882′E), from September 2011 to December 2013. With the exception of removal experiments (see below), all work was conducted within a focal colony of *N. pulcher* that contained between 135 (2011) and 153 (2013) groups, at 10–12 m depth. In this colony, all group sizes were known and we mapped the position of all territories. We calculated lateral distances between all territories (centre to centre) within the focal colony, based on each territory's position. The removal experiments were conducted in several other colonies at 10–14 m depth within approximately 200 m from the above-mentioned colony.

Study Species

In *N. pulcher*, breeding groups consist of a dominant pair largely monopolizing reproduction and several subordinates of both sexes and of varying age and size (Duftner et al., 2007; Taborsky & Limberger, 1981; Wong & Balshine, 2011a). These groups defend territories against foreign conspecifics and other species, and access to shelters provided in these territories and protection by larger group members are crucial for individual survival (Balshine et al., 2001; Heg, Bachar, Brouwer, & Taborsky, 2004; Taborsky, 1984). Subordinates help dominants to raise broods in order to be tolerated in their territory (Balshine-Earn et al., 1998; Fischer et al., 2014; Heg & Taborsky, 2010; Taborsky, 1985; Zöttl, Heg, Chervet, & Taborsky, 2013). Groups are organized in a size-based hierarchy (Dey et al., 2013; Wong & Balshine, 2011b), and higher ranking subordinates are more likely to seize dominance when breeders disappear (Stiver et al., 2006). The fish frequently visit foreign groups, which seems to familiarize them with their neighbours and allows them to seek shelter in these neighbouring territories when threatened (Bergmüller, Heg, Peer, et al., 2005). During such forays, the fish adopt a certain posture, characterized by spreading their fins and stiffening their body, propelling themselves mainly by thrusts of their pectoral fins. Thus, prospecting forays can be distinguished from other territory intrusions, and the distinct posture apparently functions as an aggression-reducing signal to resident fish (Bergmüller, Heg, Peer, et al., 2005). It has been suggested that such visits possibly prepare individuals for future dispersal into the visited groups (Bergmüller, Heg, Peer, et al., 2005). In *N. pulcher*, dispersal typically covers short distances (mean 3.5 m, range 0.4–17.2 m; Stiver, Dierkes, Taborsky, & Balshine, 2004; Jungwirth, Zöttl, Bonfils, & Taborsky, n.d.) and individuals predominantly disperse into already existing groups. Founding of new groups is very rare and may occur in two ways: budding of established territories and dispersal of several individuals into vacant territories (Heg, Heg-Bachar, Brouwer, & Taborsky, 2008; Jungwirth & Taborsky, n.d.). Shortly prior to dispersal, individuals reduce their cooperative investment in their current group compared to individuals that remain in their