



Prospecting precedes dispersal and increases survival chances in cooperatively breeding cichlids



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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.

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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

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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

territory, rendering dispersal costly to fellow group members (Bergmüller, Heg, & Taborsky, 2005; Zöttl, Chapuis, et al., 2013).

Prospecting Behaviour, Dispersal Decisions and Survival

To unravel the long-term effects of prospecting on dispersal decisions and survival, we observed the prospecting behaviour of 155 focal individual *N. pulcher* from 73 different territories between September and October 2011, and checked their survival and dispersal until a year later. As both group size and local population density influence survival in *N. pulcher* (Balshine et al., 2001; Heg, Brouwer, Bachar, & Taborsky, 2005; Heg et al., 2008; Jungwirth & Taborsky, n.d.), we recorded the sizes of all respective groups (i.e. the number of fish >1.5 cm standard length (SL); see Fischer et al., 2014; Heg & Taborsky, 2010), and the distance to their nearest-neighbouring *N. pulcher* territory, for all but one of these territories. One territory had no neighbours within 5 m and hence we did not include the nearest-neighbour distance of this territory in our data set. Focal fish were selected to cover the whole range of observed group sizes and nearest-neighbour distances, and to include fish of varying size and dominance status. Groups with focal fish were observed twice for 30 min each, during which all forays by focal individuals from the respective group to any foreign territory were recorded. At least 48 h before the first observation, each focal fish was caught using hand nets and Plexiglas tubes (see Balshine-Earn et al., 1998). Prior to capture, we assessed each individual's status (dominant or subordinate) by observing groups for at least 5 min during which we identified the largest group member of each sex; these we considered the dominant individuals, rendering all other group members subordinates (Balshine et al., 2001; Taborsky & Limberger, 1981). Upon capture, a fish's SL (to the nearest millimetre; using a measuring board with a 1 mm grid) and sex were recorded. Further, it received an elastomer mark for individual identification (visible implant elastomer: Northwest Marine Technology, Shaw Island, WA 98286, U.S.A.), and a small fin clip was collected for DNA fingerprinting, before the fish was released in its home territory. The fish were classified as either dominant male ($N = 22$), dominant female ($N = 29$), subordinate male ($N = 55$) or subordinate female ($N = 49$).

In September 2012 we recovered all marked fish and again measured their SL and took a small fin clip. Using alleles from 13 polymorphic microsatellites (see below), we confirmed the identity of 71 fish that had been marked in 2011 and were recaptured in 2012. This provided detailed information about the relationship between their prospecting behaviour in 2011 and their dispersal until a year later. We assumed recapture probabilities to be similar between all fish, as *N. pulcher* generally show high site fidelity. We considered the remaining 84 individuals as not having survived between years for the following reasons: (1) long-distance dispersal is very rare in this species (Stiver et al., 2004; Jungwirth et al., n.d.), (2) we worked in a large subset of the population, also checking fish outside the focal colony in 2012, and (3) fish marked in 2011 were likely to have reached dominance by 2012 (Jungwirth & Taborsky, n.d.). We captured a large proportion of dominants present in the focal colony in 2012, irrespective of whether we detected marks or not (36 of 78 dominant males and 78 of 146 dominant females), reducing the odds of missing fish whose marks were lost or remained undetected.

Territory Intrusion Experiment

Using simulated territory intrusions of subordinate *N. pulcher* into foreign territories, we investigated the influence of spatial distance on social interactions between these fish (see Desjardins, Stiver, Fitzpatrick, & Balshine, 2008). The intrusion experiments

were conducted between September and November 2013. Each of 44 focal individuals (none of which were part of the prospecting observations described above) was caught and subsequently presented at two foreign territories ('presentation territories'). One of these territories was located well within typical prospecting distances (Bergmüller, Heg, Peer, et al., 2005; see Results and Fig. 1; 'within prospecting distance': mean distance from the focal fish's home territory: 0.83 m, range 0.16–2.02 m) and the other was located well outside typical prospecting distances (see Results and Fig. 1; 'outside prospecting distance': mean distance from the focal fish's home territory: 11.21 m, range 4.37–20.24 m). Upon capture, fish were transferred to a clear Plexiglas tube (9 cm diameter, 14 cm length, both ends closed with perforated lids to allow water exchange). Each fish remained in the tube until it had been presented at both presentation territories. When not being presented at a territory, the tube containing the focal fish was kept in a dark bag to reduce stress. Presentations were preceded by a 3 min habituation phase, during which the experimenter was present at the test territory, but the focal fish was still hidden in the bag. During this phase, we identified the breeding shelter of the respective presentation territory (see Heg et al., 2004). The tube containing the focal fish was then placed as close to the breeding shelter as possible, without blocking its entrance. Each presentation lasted 5 min, during which we recorded all aggressive behaviours that resident *N. pulcher* directed towards the focal fish (i.e. all aggressive displays and any attempt to ram or bite the focal fish; see Balzarini, Taborsky, Wanner, Koch, & Frommen, 2014). Subsequently, the focal individual's SL and sex were determined, before it was released back in its home territory.

Removal Experiment

To test whether subordinate *N. pulcher* voluntarily disperse and fill vacancies in neighbouring territories, and whether such dispersal increases their rank and thus enhances their chances of

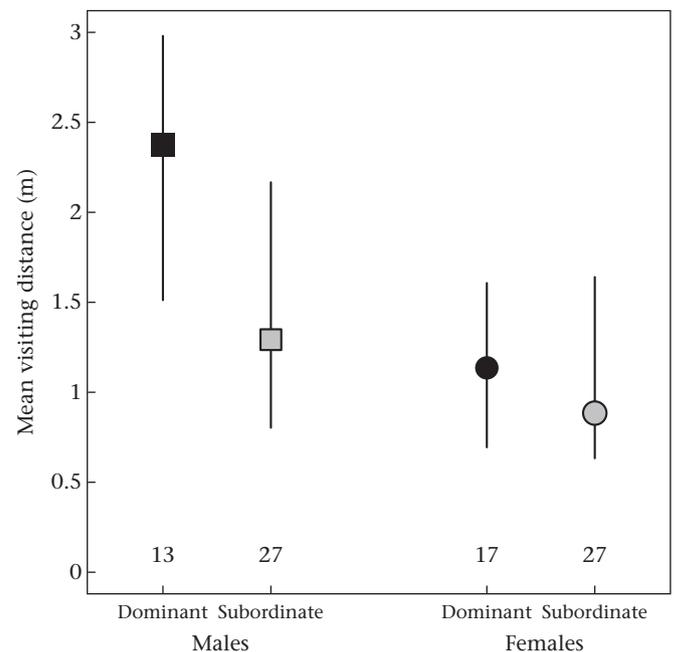


Figure 1. Mean distance a focal fish covered to visit foreign territories. Fish were classified by sex and status in their home territory (dominant or subordinate). Lines represent the interquartile range, symbols represent medians. Rectangles represent males, circles represent females. Black symbols represent dominant individuals, grey symbols represent subordinate individuals. Numbers below the boxes indicate the number of focal individuals in each class.

seizing dominance, we selected nine groups outside our focal colony in October and November 2013. We aimed to create vacancies in territories with many neighbouring groups in which potential dispersers were found, to increase the chance of actually observing voluntary dispersal. Thus, these 'central territories' (i.e. territories in which vacancies were created) were selected in a way to ensure that (1) each had at least six other territories in close proximity ('neighbouring territories'; i.e. at less than 2 m from centre to centre), and (2) in any of these neighbouring territories, there were at least three fish that fulfilled the following criteria for being chosen as focal fish: they were (a) not the largest subordinate in their respective home territory, but were (b) larger than the second largest subordinate in the 'central territory'. Thus, by removing the largest subordinate from the 'central territory', we created a vacancy that allowed focal fish to increase their rank when dispersing into it (i.e. increasing their rank from second highest or lower ranking subordinate in their home territory to highest ranking subordinate in the 'central territory'). A total of 49 fish met these criteria and were selected as focal individuals for the experiment. These fish were caught, measured, sexed and marked (see above) at least 48 h prior to the first focal observation. All focal individuals were observed for three 10 min periods prior to the removal of the largest subordinate in the 'central territory' (observations 1–3) and again for three 10 min periods after the removal (observations 4–6). See [Table 1](#) for the exact schedule.

During each observation, we recorded (1) the time a focal individual spent in its original home territory, the number of aggressive behaviours it directed (2) towards fellow group members, (3) towards foreign *N. pulcher* and (4) towards heterospecifics, (5) the number of feeding acts and (6) the number of maintenance behaviours it performed, (7) the number of submissive acts it showed, and (8) the number of forays it made to the 'central territory' (see [Bergmüller, Heg, Peer, et al., 2005](#)). Fish that were removed from the 'central territory' were caught as described above and were kept in holding cages at least 25 m from the respective 'central territory'. They were released back into their home territories at the end of the study (i.e. up to 6 weeks after their removal). We monitored the nine 'central territories' and all 49 focal individuals on a weekly basis for up to 6 weeks after the last respective observation, until the end of our field season. During these check-ups we recorded the current home territory of each focal individual and whether or not the vacancy in the 'central territory' had been filled.

DNA Fingerprinting

The following 13 microsatellite loci were used to identify individuals that were caught in different years, based on the DNA

extracted from the respective fin-clips: NP007, NP773, UL12 ([Schliewen et al., 2001](#)); Pzeb4 ([Van Oppen, Rico, Deutsch, Turner & Hewitt, 1997](#)); TmoM11, TmoM13, TmoM25, TmoM27 ([Zardoya et al., 1996](#)); UME003 ([Parker & Kornfield, 1996](#)); UNH106, UNH154 ([Lee & Kocher, 1996](#)); UNH1009 ([Carleton et al., 2002](#)); Ppun21 ([Taylor et al., 2001](#)). All loci had 2–27 alleles, with a mean of 14 alleles per locus. Identity checks were performed with the Microsatellite Toolkit, an Add-In of Microsoft Excel. DNA extraction and amplification followed the protocol described by [Bruitjes, Bonfils, Heg, and Taborsky \(2011\)](#).

Statistical Analyses

All statistical analyses were carried out using R version 3.1.1 ([R Development Core Team, 2013](#)). Generalized linear mixed-effects models (GLMM) were fitted using the R package lme4 version 1.1-6 ([Bates, Maechler, Bolker, & Walker, 2013](#)). (1) To test whether an individual's class (dominant male, dominant female, subordinate male, subordinate female) or size influenced the propensity to engage in prospecting visits, we fitted a generalized linear model (GLM) with logistic link function to account for the assumed binomial error distribution (GLM logit link). This model included one response variable (prospecting: yes/no) and two explanatory variables (class; size). (2) To test whether an individual's class or size influenced the distance covered during forays, we fitted a linear model. This model included one response variable (foray distance) and two explanatory variables (class; size). (3) To test whether individuals that survived to the next year and those that did not differed in their propensity to show prospecting behaviour, their size, their group's size or their group's nearest-neighbour distance, we fitted a GLM with logit link. This model included one response variable (survival: yes/no) and four explanatory variables (prospecting: yes/no; size; group size; nearest-neighbour distance). (4) To test whether individuals that dispersed between years and those that did not differed in their propensity to show prospecting behaviour, their size, their group's size or their group's nearest-neighbour distance, we fitted a GLM with logit link. This model included one response variable (dispersal: yes/no) and four explanatory variables (prospecting: yes/no; size; group size; nearest-neighbour distance). (5) To test whether the aggression fish received during forced intrusions was influenced by the distance to the fish's home territory, we fitted a negative binomial generalized linear mixed-effects model (GLMM NB). The model included one response variable (received aggression), one explanatory variable (distance to home territory) and a focal fish's ID as random factor.

Ethical Note

All work reported here complied with Zambian laws and was carried out in agreement with local authorities under the Memorandum of Understanding issued by the Department of Fisheries: Ministry of Agriculture and Cooperatives, Zambia, dated 20 March 2009. Fish marked for this study each received two to four elastomer tags of maximum 3 mm length in areas with minimal risk of harmful injuries, i.e. away from their internal organs (marks were placed near the dorsal and anal fin and in the tail). Fin-clips were taken from the posterior end of the dorsal fin and were less than 5 mm² in size. Both marking and fin clipping were performed without anaesthesia in order to return fish to their groups as quickly as possible (processing took less than 5 min per fish) and to minimize stress to the handled fish (anaesthetized fish may be attacked by group members before full recovery). Fish captured, marked and fin-clipped for this study were observed for at least 5 min after release and checked again ca. 24 h later. Fish typically

Table 1
Schedule of the removal experiment

Experimental day	Time	Procedure
–2 or more	Any time	Catching, marking, etc.
1	0800–1100	Observation 1
1	1500–1800	Observation 2
2	0800–1100	Observation 3
2	1500–1800	Removal
3	0800–1100	Observation 4
3	1500–1800	Observation 5
4	0800–1100	Observation 6

Each focal fish was caught at least 48 h before its first observation. Observations of 10 min each per focal individual took place either in the morning (0800–1100 hours, observations 1, 3, 4 and 6) or in the afternoon (1500–1800 hours, observations 2 and 5). The removal in the 'central territory' was conducted in the afternoon of the second experimental day. Focal fish were observed three times prior to the removal (observations 1–3) and three times after the removal (observations 4–6).

behaved normally within those 5 min, i.e. they swam freely, interacted with other group members and/or fed. No fish went missing during the first 24 h after processing. We observed no negative effects, i.e. infections, abnormal behaviour or fungal growth, caused by marking or fin clipping. In fact, clipped fins regrew completely within 3–4 weeks.

RESULTS

Effect of Social Status, Size and Prospecting

Of the 155 fish marked in 2011, 84 performed prospecting visits to foreign territories during the 60 min in which we observed their respective home territory. All classes of fish were similarly likely to perform forays to foreign territories (13 of 22 dominant males; 17 of 29 dominant females; 27 of 55 subordinate males; 27 of 49 subordinate females [class: likelihood ratio test (LRT): 2.26, $P = 0.52$]), but larger fish were more likely to perform visits than smaller ones (size: LRT: 5.26, $P = 0.022$). Visiting distances did not differ between different classes of fish (dominant males: 2.13 m, 0.97–3.64 m [median across all individual mean visiting distances, range]; dominant females: 1.14 m, 0.52–4.29 m; subordinate males: 1.29 m, 0.16–7.73 m; subordinate females: 0.88 m, 0.16–6.73 m; class: $F = 1.54$, $P = 0.19$; Fig. 1), and size did not influence visiting distances (size: $F = 1.54$, $P = 0.77$). Fish that were recaptured in 2012 ($N = 71$) differed from those that were not recovered ($N = 84$) in their propensity to perform forays (45 of 71 recaptured fish had performed visits, as had 39 of 84 fish that were not recovered; LRT: 4.19, $P = 0.041$), but not in their size (LRT: 0.65, $P = 0.42$), their group's size (LRT: 1.63, $P = 0.2$) or their group's nearest-neighbour distance (LRT: 0.41, $P = 0.52$). Of the fish that were recaptured in 2012, those that had dispersed between years ($N = 31$) did not differ from those that had not ($N = 40$) with respect to their propensity to perform forays to other groups (LRT: 0.41, $P = 0.52$), their size (LRT: 2.11, $P = 0.15$), their group's size (LRT: 0.56, $P = 0.46$) or their group's nearest-neighbour distance (LRT: 0.09, $P = 0.76$). Of 31 fish that had dispersed by 2012, 20 had been observed to perform forays to other groups, while 11 had not. Of these dispersers, one moved to a territory it had been observed to visit in 2011, while 30 dispersed into territories they had not been observed to visit during our 1 h recordings. Of 40 fish that did not disperse between years, 25 had been observed to perform forays to other groups, while 15 had not.

Effect of Distance on Received Aggression

Focal fish that were experimentally presented in a foreign territory received more aggression the further away the respective presentation territory was located from their home territory ($t = 2.11$, $P = 0.032$; Fig. 2).

Link Between Prospecting and Voluntary Dispersal

Of the nine subordinate vacancies opened by removals from 'central territories', three were taken up by subordinates joining the respective groups, while the other six remained vacant. Two of these joiners were previously marked and observed focal fish, but one was an unmarked fish of unknown origin. Of all observed focal fish, one of the marked eventual dispersers had performed by far the most forays to the respective 'central territory' prior to the removal (a total of nine visits), whereas the other marked disperser had not been observed visiting the 'central territory' prior to the removal. Of the 47 fish that stayed in their original territory, 42 had not visited the 'central territory' prior to the removal, whereas five had (albeit at low frequencies: one or two visits each). Both

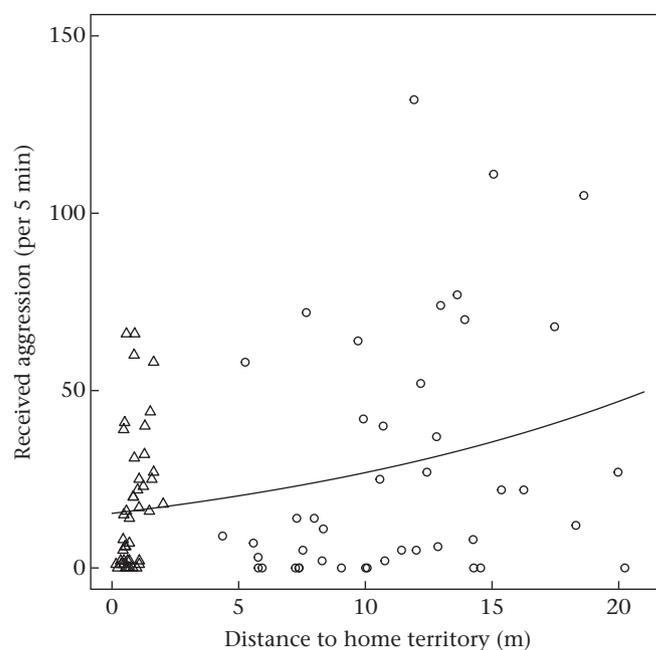


Figure 2. Number of aggressive behaviours the focal fish received during 5 min of presentation in a foreign territory as a function of distance between the focal fish's home territory and the presentation territory. Triangles represent the aggression an individual focal fish received at a 'within prospecting distance' territory, circles represent the aggression an individual focal fish received at an 'outside prospecting distance' territory.

eventual dispersers made forays to the respective 'central territory' after the removal (two and 12 visits, respectively), as did nine other individuals (one or two visits each), whereas 38 individuals did not visit the respective 'central territory' after the removal (a total of 34 individuals were never observed to make forays; Table 2). Notably, the two fish that eventually dispersed into the 'central territory' spent most of the postremoval observation time (observations 4–6) in their original home territory (1392 and 1715 of 1800 s, respectively). Thus, the actual dispersal (classified as the focal fish spending most time in the 'central territory') was only detected during the first check a week after the removal. All of the 47 fish that did not disperse to the 'central territory' stayed in their original territories for the remainder of our field season (i.e. for up to 6 weeks after the removal).

DISCUSSION

Our results show that prospecting behaviour in *N. pulcher* serves multiple purposes. Prospecting seems to provide survival benefits, as fish that performed forays to foreign groups in one year were more likely to survive to the next year. This benefit of prospecting was probably caused by increased familiarity between individuals from different groups, which allows individuals to seek shelter in foreign territories more easily (see Bergmüller, Heg, Peer, et al., 2005). This interpretation is further supported by the observation that fish typically visited nearby territories, and that they received less aggression at nearer territories when experimentally forced to intrude into them. While fish did not overall receive more aggression at territories outside typical prospecting distances compared to territories within such distances, global aggression levels increased with geographical distance between the respective presentation territory and the home territory.

Given the apparent positive effects of prospecting for survival, it is unclear why nearly half of the focal fish were not observed to

Table 2
Behavioural measurements of 49 subordinate *N. pulcher* belonging to territories in the vicinity of the 'central territory' in which a vacancy was created by removal of a large subordinate

Behaviour	Prior to removal			After removal		
	Stay: 0V	Stay: V	Disperse	Stay: 0V	Stay: V	Disperse
Number of individuals	42	5	2	42	5	2
Time on territory	1508.14	1451.8	1401.5	1541.12	1559	1553.5
Aggression towards group members	4.24	6.4	4	2.88	3.8	3.5
Aggression towards foreign conspecifics	5.24	3.4	2	3.64	7.8	5.5
Aggression towards heterospecifics	5.31	6.4	7	4.60	10.6	1
Feeding events	1115.33	834.8	1191	915.07	810.2	867
Maintenance	5	4.2	0	6.55	6.2	1.5
Submission	4.90	5	6	4.14	2.6	5
Visits to central territory	0	1.2	4.5	0.29	0.2	7

Behaviours were recorded during three 10 min (1800 s) focal observations prior to the removal and three 10 min focal observations after the removal. Forty-two individuals remained in their home territory throughout the observation period and did not perform any prospecting visits to the 'central territory' prior to the removal (Stay: 0V), five individuals remained in their home territory throughout the observation period, but did perform prospecting to the 'central territory' prior to the removal (Stay: V) and two individuals dispersed to the 'central territory' (Disperse). Measurements are given as means over all respective individuals and observations, i.e. per 1800 s (time on territory: s; aggression towards group members/aggression towards foreign conspecifics/aggression towards heterospecifics: number of agonistic behaviours; feeding events: number of feeding behaviours; maintenance: number of maintenance behaviours; submission: number of submissive behaviours; visits to central territory: number of forays to the 'central territory').

make forays to foreign groups during our surveys, which suggests that their prospecting propensity was relatively low. There are at least two possible explanations for this individual variation in prospecting propensity. First, it is likely that forays are costly due to increased risk and increased expenditure of time and energy, so that only individuals of high quality or those in good condition are able to afford to make them. The observed correlation between survival and prospecting might hence result from differences in quality between our focal fish. Second, fish might gain short-term benefits from abstaining from visiting behaviour, for instance because they can then better focus on within-group relationships. Experimental manipulations of prospecting behaviour will be needed to clarify which possibility is more likely to explain the observed variation in prospecting propensity.

Previous research has shown that in many species prospecting precedes dispersal, and that information gathered during prospecting is used to make dispersal decisions (Clobert et al., 2009). For example, dispersal may be directed predominantly towards sites that have previously been prospected (Bergmüller, Heg, Peer, et al., 2005; Dittmann et al., 2007), prospecting may be most common at successful breeding sites (Calabuig, Ortego, Aparicio, & Cordero, 2010; Pärt & Doligez, 2003) and individuals that prospect more may be more likely to disperse (Ward, 2005). Thus, we expected those *N. pulcher* that had been observed to make more forays to foreign groups to be more likely to disperse between years, and to preferentially direct dispersal to previously visited territories. However, across longer time periods individual differences in prospecting behaviour did not predict future dispersal decisions in our study: fish that had made more forays in one year were not more likely to have dispersed by the next year, and dispersers did not preferentially join groups they had visited during our focal observations a year before. However, in the removal experiment one of the two eventually successful dispersers had visited the target territory frequently prior to the removal. In addition, dispersal events observed in the removal experiment stretched over several days before the respective focal fish actually spent most of its time in the target territory. During this time, focal fish repeatedly prospected the eventual target territory. Thus, while prospecting appears to increase familiarity between individual *N. pulcher* from different groups, its role for dispersal decisions cannot be easily unveiled. In fact, an individual's decision to disperse to a new territory appears to be opportunistic and observable behavioural changes take place only shortly before the actual dispersal event (see Zöttl, Chapuis, et al., 2013; similar to meerkats, *Suricata suricatta*: Mares, Bateman, English, Clutton-

Brock, & Young, 2014). Given the frequent observation of predisposed dispersal phenotypes in many animal species and their adaptive benefits (Bonte et al., 2012; Chapman et al., 2011; Clobert et al., 2009; Fjerdingstad, Schtickzelle, Manhes, Gutierrez, & Clobert, 2007; Tarwater & Beissinger, 2012), it is somewhat surprising that in *N. pulcher* individuals do not appear to be strongly predisposed to one of two life history trajectories: dispersing or queuing (but see Bergmüller & Taborsky, 2007 for divergent experimental evidence).

In cooperative species, it may not pay to be predictable with respect to dispersal decisions for at least three nonmutually exclusive reasons. First, as outlined above, dispersal introduces a conflict of interest between fellow group members. A future disperser should aim to reduce investment in the current group, while current group members should discriminate against individuals that invest too little in the common good and punish or evict them (Cant et al., 2001; Fischer et al., 2014; Taylor, Rodrigues, Gardner, & Buckling, 2013; Tibbetts, 2007; Zöttl, Chapuis, et al., 2013). To avoid these costly consequences, it may be in a future disperser's best interest to conceal its intentions (Queller & Strassmann, 2013). Second, dispersal appears to be the less preferred life history trajectory in many cooperative species, where individuals that stay with their natal group fare better (Cockburn, 1998; Covas & Griesser, 2007; Griesser, Nystrand, & Ekman, 2006; Pasinelli & Walters, 2002; Robbins & Robbins, 2005; Sparkman, Adams, Steury, Waits, & Murray, 2010; Stacey & Ligon, 1991). Thus, dispersal events often seem to be opportunistic and/or dependent on unpredictable events, e.g. the opening of a breeding vacancy in a foreign group, or expulsion from the natal group. Third, it may pay to sustain good relations with the former group even after dispersal. This is because the former group may now serve as a safe haven, or because the dispersal turns out to not be beneficial. In fact, we have observed fish that had dispersed to frequently visit their former group, and to occasionally rejoin their former groups after already spending several weeks in the new group. Consequently, an individual's best bet may be to fully commit to its current group as long as it has not finally decided to disperse. For these reasons, committing to dispersal as a life history trajectory early on may be maladaptive in cooperative species, while the costs outlined above do not apply to systems that do not rely on within-group cooperation for survival and reproduction.

Our results suggest that prospecting may directly benefit individuals by raising their survival chances. Our results further provide evidence that prospecting may be part of the preparation for dispersal in cooperative breeders. In highly social species,

dispersal can be a complex process, as the success and payoff of dispersal are dependent on members of groups that dispersers leave and members of groups that dispersers join. Hence, a wide range of social interactions needs to be considered when individuals prepare for this important life history decision.

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References

- Balshine-Earn, S., Neat, F., Reid, H., & Taborsky, M. (1998). Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. *Behavioral Ecology*, 9(5), 432–438. <http://dx.doi.org/10.1093/beheco/9.5.432>.
- Balshine, S., Leach, B., Neat, F., Reid, H., Taborsky, M., & Werner, N. Y. (2001). Correlates of group size in a cooperatively breeding cichlid fish (*Neolamprologus pulcher*). *Behavioral Ecology and Sociobiology*, 50(2), 134–140. <http://dx.doi.org/10.1007/s002650100343>.
- Balzarini, V., Taborsky, M., Wanner, S., Koch, F., & Frommen, J. G. (2014). Mirror, mirror on the wall: the predictive value of mirror tests for measuring aggression in fish. *Behavioral Ecology and Sociobiology*, 68(5), 871–878. <http://dx.doi.org/10.1007/s00265-014-1698-7>.
- Barber, I., & Wright, H. A. (2001). How strong are familiarity preferences in shoaling fish? *Animal Behaviour*, 61(5), 975–979. <http://dx.doi.org/10.1006/anbe.2000.1665>.
- Bates, D., Maechler, M., Bolker, B. M., & Walker, S. (2013). *lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7*. <http://cran.r-project.org/package=lme4>.
- Bergmüller, R., Heg, D., Peer, K., & Taborsky, M. (2005). Extended safe havens and between-group dispersal of helpers in a cooperatively breeding cichlid. *Behaviour*, 142, 1643–1667.
- Bergmüller, R., Heg, D., & Taborsky, M. (2005). Helpers in a cooperatively breeding cichlid stay and pay or disperse and breed, depending on ecological constraints. *Proceedings of the Royal Society B: Biological Sciences*, 272(1560), 325–331. <http://dx.doi.org/10.1098/rspb.2004.2960>.
- Bergmüller, R., & Taborsky, M. (2007). Adaptive behavioural syndromes due to strategic niche specialization. *BMC Ecology*, 7(12), 1–7. <http://dx.doi.org/10.1186/1472-6785-7-12>.
- Bocedi, G., Heinonen, J., & Travis, J. M. J. (2012). Uncertainty and the role of information acquisition in the evolution of context-dependent emigration. *The American Naturalist*, 179(5), 606–620. <http://dx.doi.org/10.1086/665004>.
- Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M. M., Gibbs, M., et al. (2012). Costs of dispersal. *Biological Reviews of the Cambridge Philosophical Society*, 87(2), 290–312. <http://dx.doi.org/10.1111/j.1469-185X.2011.00201.x>.
- Boulinier, T., McCoy, K. D., Yoccoz, N. G., Gasparini, J., & Tveraa, T. (2008). Public information affects breeding dispersal in a colonial bird: kittiwakes cue on neighbours. *Biology Letters*, 4, 538–540. <http://dx.doi.org/10.1098/rsbl.2008.0291>.
- Bruintjes, R., Bonfils, D., Heg, D., & Taborsky, M. (2011). Paternity of subordinates raises cooperative effort in cichlids. *PLoS One*, 6(10), e25673. <http://dx.doi.org/10.1371/journal.pone.0025673>.
- Calabuig, G., Ortego, J., Aparicio, J. M., & Cordero, P. J. (2010). Intercolony movements and prospecting behaviour in the colonial lesser kestrel. *Animal Behaviour*, 79, 811–817. <http://dx.doi.org/10.1016/j.anbehav.2009.12.007>.
- Cant, M. A. (2011). The role of threats in animal cooperation. *Proceedings of the Royal Society B: Biological Sciences*, 278(1703), 170–178. <http://dx.doi.org/10.1098/rspb.2010.1241>.
- Cant, M. A., Otafi, E., & Mwanguhya, F. (2001). Eviction and dispersal in cooperatively breeding banded mongooses (*Mungos mungo*). *Journal of Zoology*, 254(2), 155–162. <http://dx.doi.org/10.1017/S0952836901000668>.
- Carleton, K. L., Strelman, J. T., Lee, B. Y., Garnhart, N., Kidd, M., & Kocher, T. D. (2002). Rapid isolation of CA microsatellites from the tilapia genome. *Animal Genetics*, 33, 140–144. <http://dx.doi.org/10.1046/j.1365-2052.2002.00817.x>.
- Carter, G. G., & Wilkinson, G. S. (2013). Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20122573.
- Chapman, B. B., Hulthén, K., Blomqvist, D. R., Hansson, L.-A., Nilsson, J.-Å., Brodersen, J., et al. (2011). To boldly go: individual differences in boldness influence migratory tendency. *Ecology Letters*, 871–876. <http://dx.doi.org/10.1111/j.1461-0248.2011.01648.x>.
- Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S., & Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, 12(3), 197–209. <http://dx.doi.org/10.1111/j.1461-0248.2008.01267.x>.
- Clutton-Brock, T. H. (1998). Reproductive skew, concessions and limited control. *Trends in Ecology & Evolution*, 13(7), 288–292.
- Cockburn, A. (1998). Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics*, 29, 141–177.
- Covas, R., & Griesser, M. (2007). Life history and the evolution of family living in birds. *Proceedings of the Royal Society B: Biological Sciences*, 274, 1349–1357. <http://dx.doi.org/10.1098/rspb.2007.0117>.
- Cox, A. S., & Kesler, D. C. (2012). Prospecting behavior and the influence of forest cover on natal dispersal in a resident bird. *Behavioral Ecology*, 23(5), 1068–1077. <http://dx.doi.org/10.1093/beheco/ars076>.
- Daniels, S. J., & Walters, J. R. (2000). Between-year breeding dispersal in red-cockaded woodpeckers: multiple causes and estimated cost. *Ecology*, 81(9), 2473–2484.
- Delgado, M. M., Barton, K. A., Bonte, D., & Travis, J. M. J. (2014). Prospecting and dispersal: their eco-evolutionary dynamics and implications for population patterns. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20132851.
- Desjardins, J. K., Stiver, K., Fitzpatrick, J., & Balshine, S. (2008). Differential responses to territory intrusions in cooperatively breeding fish. *Animal Behaviour*, 75(2), 595–604. <http://dx.doi.org/10.1016/j.anbehav.2007.05.025>.
- Dey, C. J., Reddon, A. R., O'Connor, C. M., & Balshine, S. (2013). Network structure is related to social conflict in a cooperatively breeding fish. *Animal Behaviour*, 85(2), 395–402. <http://dx.doi.org/10.1016/j.anbehav.2012.11.012>.
- Dittmann, T., Ezaard, T. H. G., & Becker, P. H. (2007). Prospectors' colony attendance is sex-specific and increases future recruitment chances in a seabird. *Behavioural Processes*, 76(3), 198–205. <http://dx.doi.org/10.1016/j.beproc.2007.05.002>.
- Doolan, S. P., & Macdonald, D. W. (1996). Dispersal and extra-territorial prospecting by slender-tailed meerkats (*Suricata suricatta*) in the south-western Kalahari. *Journal of Zoology*, 240, 59–73.
- Duftner, N., Sefc, K. M., Koblmüller, S., Salzburger, W., Taborsky, M., & Sturmbauer, C. (2007). Parallel evolution of facial stripe patterns in the *Neolamprologus brichardi/pulcher* species complex endemic to Lake Tanganyika. *Molecular Phylogenetics and Evolution*, 45(2), 706–715. <http://dx.doi.org/10.1016/j.jmpev.2007.08.001>.
- Fischer, S., Zöttl, M., Groenewoud, F., & Taborsky, B. (2014). Group-size-dependent punishment of idle subordinates in a cooperative breeder where helpers pay to stay. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20140184.
- Fjerdingstad, E. J., Schtickzelle, N., Manhes, P., Gutierrez, A., & Clobert, J. (2007). Evolution of dispersal and life history strategies – *Tetrahymena ciliates*. *BMC Evolutionary Biology*, 7(133). <http://dx.doi.org/10.1186/1471-2148-7-133>.
- Glander, K. E. (1992). Dispersal patterns in Costa Rican mantled howling monkeys. *International Journal of Primatology*, 13(4), 415–436.
- Griesser, M., Nystrand, M., & Ekman, J. (2006). Reduced mortality selects for family cohesion in a social species. *Proceedings of the Royal Society B: Biological Sciences*, 273, 1881–1886. <http://dx.doi.org/10.1098/rspb.2006.3527>.
- Heg, D., Bachar, Z., Brouwer, L., & Taborsky, M. (2004). Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid. *Proceedings of the Royal Society B: Biological Sciences*, 271, 2367–2374. <http://dx.doi.org/10.1098/rspb.2004.2855>.
- Heg, D., Brouwer, L., Bachar, Z., & Taborsky, M. (2005). Large group size yields group stability in the cooperatively breeding cichlid *Neolamprologus pulcher*. *Behaviour*, 142, 1615–1641.
- Heg, D., Heg-Bachar, Z., Brouwer, L., & Taborsky, M. (2008). Experimentally induced helper dispersal in colonially breeding cooperative cichlids. *Environmental Biology of Fishes*, 83(2), 191–206. <http://dx.doi.org/10.1007/s10641-007-9317-3>.
- Heg, D., & Taborsky, M. (2010). Helper response to experimentally manipulated predation risk in the cooperatively breeding cichlid *Neolamprologus pulcher*. *PLoS One*, 5(5), e10784. <http://dx.doi.org/10.1371/journal.pone.0010784>.
- Hopp, S. L., Jablonski, P., & Brown, J. L. (2001). Recognition of group membership by voice in Mexican jays, *Aphelocoma ultramarina*. *Animal Behaviour*, 62(2), 297–303. <http://dx.doi.org/10.1006/anbe.2001.1745>.
- Johannesen, J., & Lubin, Y. (1999). Group founding and breeding structure in the subsocial spider *Stegodyphus lineatus* (Eresidae). *Heredity*, 82, 677–686.
- Jordan, L. A., Wong, M., & Balshine, S. (2010). The effects of familiarity and social hierarchy on group membership decisions in a social fish. *Biology Letters*, 6(3), 301–303. <http://dx.doi.org/10.1098/rsbl.2009.0732>.
- Jungwirth, A., & Taborsky, M. (n.d.). [Long-term field data on demographic changes in a colony of cooperatively breeding cichlids]. Unpublished raw data.
- Jungwirth, A., Zöttl, M., Bonfils, D., & Taborsky, M. (n.d.). [Long-term field data on individual dispersal decisions in a cooperatively breeding cichlid]. Unpublished raw data.
- Keller, L., & Ross, K. G. (1998). Selfish genes: a green beard in the red fire ant. *Nature*, 251, 573–575.
- Kesler, D. C., & Haig, S. M. (2007). Territoriality, prospecting, and dispersal in cooperatively breeding Micronesian kingfishers (*Todiramphus cinnamominus reichenbachii*). *The Auk*, 124(2), 381–395.
- Krams, I., Krama, T., Igaune, K., & Mänd, R. (2007). Experimental evidence of reciprocal altruism in the pied flycatcher. *Behavioral Ecology and Sociobiology*, 62(4), 599–605. <http://dx.doi.org/10.1007/s00265-007-0484-1>.
- Lee, W. J., & Kocher, T. D. (1996). Microsatellite DNA markers for genetic mapping in *Oreochromis niloticus*. *Journal of Fish Biology*, 49, 169–171. <http://dx.doi.org/10.1111/j.1095-8649.1996.tb00014.x/abstract>.
- Lehmann, L., & Perrin, N. (2002). Altruism, dispersal, and phenotype-matching kin recognition. *The American Naturalist*, 159(5), 451–468. <http://dx.doi.org/10.1086/339458>.

- Mares, R., Bateman, A. W., English, S., Clutton-Brock, T. H., & Young, A. J. (2014). Timing of predispersal prospecting is influenced by environmental, social and state-dependent factors in meerkats. *Animal Behaviour*, 88, 185–193. <http://dx.doi.org/10.1016/j.anbehav.2013.11.025>.
- McDonald, P. G. (2012). Cooperative bird differentiates between the calls of different individuals, even when vocalizations were from completely unfamiliar individuals. *Biology Letters*, 8(3), 365–368. <http://dx.doi.org/10.1098/rsbl.2011.1118>.
- Parker, A., & Kornfield, I. (1996). Polygynandry in *Pseudotropheus zebra*, a cichlid fish from Lake Malawi. *Environmental Biology of Fishes*, 47, 345–352.
- Pärt, T., & Doligez, B. (2003). Gathering public information for habitat selection: prospecting birds cue on parental activity. *Proceedings of the Royal Society B: Biological Sciences*, 270, 1809–1813. <http://dx.doi.org/10.1098/rspb.2003.2419>.
- Pasinelli, G., & Walters, J. R. (2002). Social and environmental factors affect natal dispersal and philopatry of male red-cockaded woodpeckers. *Ecology*, 83(8), 2229–2239. [http://dx.doi.org/10.1890/0012-9658\(2002\)083\[2229:SAEFAN\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2002)083[2229:SAEFAN]2.0.CO;2).
- Payne, R. B., Payne, L. L., Rowley, L., & Russell, E. M. (1991). Social recognition and response to song in cooperative red-winged fairy-wrens. *The Auk*, 108(4), 811–819.
- Ponchon, A., Garnier, R., Grémillet, D., & Boulinier, T. (2015). Predicting population responses to environmental change: the importance of considering informed dispersal strategies in spatially structured population models. *Diversity and Distributions*, 21, 88–100. <http://dx.doi.org/10.1111/ddi.12273>.
- Queller, D. C., & Strassmann, J. E. (2013). The veil of ignorance can favour biological cooperation. *Biology Letters*, 9, 20130365. <http://dx.doi.org/10.1098/rsbl.2013.0365>.
- R Development Core Team. (2013). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.r-project.org/>.
- Radford, A. N. (2005). Group-specific vocal signatures and neighbour–stranger discrimination in the cooperatively breeding green woodhoopoe. *Animal Behaviour*, 70(5), 1227–1234. <http://dx.doi.org/10.1016/j.anbehav.2005.04.002>.
- Reber, A., Meunier, J., & Chapuisat, M. (2010). Flexible colony-founding strategies in a socially polymorphic ant. *Animal Behaviour*, 79(2), 467–472. <http://dx.doi.org/10.1016/j.anbehav.2009.11.030>.
- Robbins, A. M., & Robbins, M. M. (2005). Fitness consequences of dispersal decisions for male mountain gorillas (*Gorilla beringei beringei*). *Behavioral Ecology and Sociobiology*, 58(3), 295–309. <http://dx.doi.org/10.1007/s00265-005-0917-7>.
- Roberts, G., & Sherratt, T. N. (1998). Development of cooperative relationships through increasing investment. *Nature*, 394, 175–179.
- Ronce, O. (2007). How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology, Evolution, and Systematics*, 38(1), 231–253. <http://dx.doi.org/10.1146/annurev.ecolsys.38.091206.095611>.
- Rood, J. P. (1987). Dispersal and intergroup transfer in the dwarf mongoose. In B. D. Chepko-Sade, & Z. T. Halpin (Eds.), *Mammalian dispersal patterns: The effects of social structure on population genetics* (pp. 85–103). Chicago, IL: University of Chicago Press.
- Schliwien, U., Rassmann, K., Markmann, M., Markert, J., Kocher, T. D., & Tautz, D. (2001). Genetic and ecological divergence of a monophyletic cichlid species pair under fully sympatric conditions in Lake Ejagham, Cameroon. *Molecular Ecology*, 10, 1471–1488. <http://dx.doi.org/10.1046/j.1365-294X.2001.01276.x>.
- Sharp, S. P., Simeoni, M., & Hatchwell, B. J. (2008). Dispersal of sibling coalitions promotes helping among immigrants in a cooperatively breeding bird. *Proceedings of the Royal Society B: Biological Sciences*, 275(1), 2125–2130. <http://dx.doi.org/10.1098/rspb.2008.0398>.
- Smukalla, S., Caldara, M., Pochet, N., Beauvais, A., Guadagnini, S., Yan, C., et al. (2008). FLO1 is a variable green beard gene that drives biofilm-like cooperation in budding yeast. *Cell*, 135(4), 726–737. <http://dx.doi.org/10.1016/j.cell.2008.09.037>.
- Sparkman, A. M., Adams, J. R., Steury, T. D., Waits, L. P., & Murray, D. L. (2010). Direct fitness benefits of delayed dispersal in the cooperatively breeding red wolf (*Canis rufus*). *Behavioral Ecology*, 22(1), 199–205. <http://dx.doi.org/10.1093/beheco/arq194>.
- Stacey, P. B., & Ligon, J. D. (1991). The Benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. *The American Naturalist*, 137(6), 831–846.
- Stiver, K., Dierkes, P., Taborsky, M., & Balshine, S. (2004). Dispersal patterns and status change in a co-operatively breeding cichlid *Neolamprologus pulcher*: evidence from microsatellite analyses and behavioural observations. *Journal of Fish Biology*, 65, 91–105. <http://dx.doi.org/10.1111/j.1095-8649.2004.00427.x>.
- Stiver, K., Fitzpatrick, J., Desjardins, J. K., & Balshine, S. (2006). Sex differences in rates of territory joining and inheritance in a cooperatively breeding cichlid fish. *Animal Behaviour*, 71(2), 449–456. <http://dx.doi.org/10.1016/j.anbehav.2005.06.011>.
- Strassmann, J. E., Gilbert, O. M., & Queller, D. C. (2011). Kin discrimination and cooperation in microbes. *Annual Review of Microbiology*, 65, 349–367. <http://dx.doi.org/10.1146/annurev.micro.112408.134109>.
- Sturgis, S. J., & Gordon, D. M. (2012). Nestmate recognition in ants (Hymenoptera: Formicidae): a review. *Myrmecological News*, 16, 101–110.
- Taborsky, M. (1984). Broodcare helpers in the cichlid fish *Lamprologus brichardi*: their costs and benefits. *Animal Behaviour*, 32(4), 1236–1252.
- Taborsky, M. (1985). Breeder-helper conflict in a cichlid fish with broodcare helpers: an experimental analysis. *Behaviour*, 95(1), 45–75.
- Taborsky, M., & Limberger, D. (1981). Helpers in fish. *Behavioral Ecology and Sociobiology*, 8, 143–145.
- Taborsky, B., & Oliveira, R. F. (2012). Social competence: an evolutionary approach. *Trends in Ecology & Evolution*, 27(12), 679–688. <http://dx.doi.org/10.1016/j.tree.2012.09.003>.
- Tarwater, C. E., & Beissinger, S. R. (2012). Dispersal polymorphisms from natal phenotype-environment interactions have carry-over effects on lifetime reproductive success of a tropical parrot. *Ecology Letters*, 15(11), 1218–1229. <http://dx.doi.org/10.1111/j.1461-0248.2012.01843.x>.
- Taylor, M. I., Meardon, F., Turner, G. F., Seehausen, O., Mrosso, H. D. J., & Rico, C. (2001). Polymorphic microsatellite markers in the spider *Pholcus phalangioides* isolated from a library enriched for CA repeats. *Molecular Ecology Notes*, 1, 255–257. <http://dx.doi.org/10.1046/j.1471-8278>.
- Taylor, T. B., Rodrigues, A. M. M., Gardner, A., & Buckling, A. (2013). The social evolution of dispersal with public goods cooperation. *Journal of Evolutionary Biology*, 26(12), 2644–2653. <http://dx.doi.org/10.1111/jeb.12259>.
- Tibbetts, E. A. (2007). Dispersal decisions and predispersal behavior in *Polistes* paper wasp “workers.” *Behavioral Ecology and Sociobiology*, 61(12), 1877–1883. <http://dx.doi.org/10.1007/s00265-007-0427-x>.
- Van Oppen, M. J., Rico, C., Deutsch, J. C., Turner, G. F., & Hewitt, G. M. (1997). Isolation and characterization of microsatellite loci in the cichlid fish *Pseudotropheus zebra*. *Molecular Ecology*, 6, 387–388. <http://dx.doi.org/10.1046/j.1365-294X.1997.00188.x>.
- Ward, M. P. (2005). Habitat selection by dispersing yellow-headed blackbirds: evidence of prospecting and the use of public information. *Oecologia*, 145, 650–657. <http://dx.doi.org/10.1007/s00442-005-0179-0>.
- Wong, M., & Balshine, S. (2011a). Fight for your breeding right: hierarchy re-establishment predicts aggression in a social queue. *Biology Letters*, 7, 190–193. <http://dx.doi.org/10.1098/rsbl.2010.0639>.
- Wong, M., & Balshine, S. (2011b). The evolution of cooperative breeding in the African cichlid fish, *Neolamprologus pulcher*. *Biological Reviews of the Cambridge Philosophical Society*, 86(2), 511–530. <http://dx.doi.org/10.1111/j.1469-185X.2010.00158.x>.
- Young, A. J., Carlson, A. A., & Clutton-Brock, T. H. (2005). Trade-offs between extraterritorial prospecting and helping in a cooperative mammal. *Animal Behaviour*, 70(4), 829–837. <http://dx.doi.org/10.1016/j.anbehav.2005.01.019>.
- Young, A. J., Spong, G., & Clutton-Brock, T. H. (2007). Subordinate male meerkats prospect for extra-group paternity: alternative reproductive tactics in a cooperative mammal. *Proceedings of the Royal Society B: Biological Sciences*, 274, 1603–1609. <http://dx.doi.org/10.1098/rspb.2007.0316>.
- Zack, S., & Rabenold, K. N. (1989). Assessment, age and proximity in dispersal contests among cooperative wrens: field experiments. *Animal Behaviour*, 38, 235–247.
- Zardoya, R., Vollmer, D. M., Craddock, C., Strelman, J. T., Karl, S., & Meyer, A. (1996). Evolutionary conservation of microsatellite flanking regions and their use in resolving the phylogeny of cichlid fishes (Pisces: Perciformes). *Proceedings of the Royal Society B: Biological Sciences*, 263(1376), 1589–1598.
- Zöttl, M., Chapuis, L., Freiburghaus, M., & Taborsky, M. (2013). Strategic reduction of help before dispersal in a cooperative breeder. *Biology Letters*, 9(1), 20120878.
- Zöttl, M., Heg, D., Chervet, N., & Taborsky, M. (2013). Kinship reduces alloparental care in cooperative cichlids where helpers pay-to-stay. *Nature Communications*, 4, 1341. <http://dx.doi.org/10.1038/ncomms2344>.