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Social stability in times of change: effects of group fusion and water depth on sociality in a globally invasive fish

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Many animals form dynamic societies in which the fission and fusion of subgroups occurs on a regular basis. Such societies are intriguing, because it is unclear whether stable dominance relationships that form within subgroups are retained upon fusion with other subgroups, and what the implications of rank instability may be at higher levels of ecological organization. Additionally, little is known about how environmental change affects the fission–fusion process, even though environments often fluctuate and are predicted to become increasingly variable, in part due to climate change. Here we investigated the social organization, levels of conflict and stability of dominance relationships during group fusion in a globally invasive fish, the eastern mosquitofish, *Gambusia holbrooki*. To assess the effect of environmental variation, we conducted group fusion experiments at high and low water depths, to simulate normal and drought conditions, and recorded dominance interactions during prefusion, early fusion and late fusion stages. Individuals formed size-based hierarchies within prefusion groups, although the relationship between size and dominance varied with group fusion. Levels of conflict were affected by group fusion and water depth, with higher levels of conflict after fusion and at low depth. Rank relationships in early and late fusion groups were stable and unaffected by water depth. Finally, there was no evidence of coat-tail effects, as familiarity with the alpha dominant in postfusion groups did not lead to a significant increase in subordinate dominance rank. All in all, these results provide key experimental evidence that environmental change in terms of water level is unlikely to impact social organization or rank stability in response to group fusion in this species. More generally, they indicate that sociality in fission–fusion societies may be relatively robust to changes in both social and environmental contexts.

Many animals form stable social groups in which individuals spend most if not their entire lives interacting with the same group members and group membership is strictly regulated (e.g. Bourke, 1997; Emlen, 1995; Wong & Buston, 2013). Others, by contrast, form more dynamic societies in which group size and composition frequently vary owing to the splitting (fission) and coalescing (fusion) of temporary subgroups, sometimes over relatively short timescales (Aureli et al., 2008; Couzin, 2006; Smith, Kolowski, Graham, Dawes, & Holekamp, 2008). These fission–fusion societies have been documented in a range of taxa typically exhibiting high sociocognitive abilities, such as birds, primates, cetaceans and ungulates (Fishlock & Lee, 2013; Parra, Corkeron, & Arnold, 2011; Ren, Li, Garber, & Li, 2012; Silk, Croft, Tregenza, & Bearhop, 2014; Smith et al., 2008). However, the phenomenon has also been reported in species with more limited cognitive abilities, such as social insects and fishes (Croft et al., 2003; Dugatkin, Alfieri, & Moore, 1994; Krause, Butlin, Peuhkuri, & Pritchard, 2000).

One aspect of fission–fusion societies that has generated keen interest lies in understanding whether the integrity of original rank relationships is maintained when two or more existing dominance hierarchies merge. Studies addressing the question of rank acquisition and stability have typically utilized long-term observations combined with analyses of patterns of interindividual interactions in natural systems (e.g. Amici, Aureli, & Call, 2008; Carter, Seddon, Frére, Carter, & Goldizen, 2013; Fishlock & Lee, 2013; Kerth, Perony, & Schweitzer, 2011; Silk et al., 2014). However, there appears to be taxonomic variation in the tendency for rank relationships to stabilize or destabilize during fission–fusion events (Gueron & Levin, 1995; Parra et al., 2011). For example, Parra et al. (2011) found that social relationships of the Indo-Pacific humpback dolphin, *Sousa chinensis*, were short-term and temporally unstable in contrast with the Australian snubfin dolphin, *Orcaella heinsohni*, which

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showed increased stability of rank relationships and associations. As such, rank relationships may not necessarily be stable in the face of changes in social context, even between ecologically similar species.

Experiments in which stable subgroups fuse under controlled conditions have also been useful for testing the influence of individual level traits on rank acquisition and stability after fusion, although these studies are comparatively few. Earley and Dugatkin (2006) observed that dominance ranks among green swordtail fish, *Xiphophorus helleri*, were highly consistent between prefusion and postfusion groups. One possible mechanism for this stability is an overriding effect of relative body size which did predict postfusion ranks, with larger individuals achieving higher ranks in the postfusion groups. Indeed, for many animals, size could play an important role in the maintenance of ranks despite a shifting composition of familiar and unfamiliar conspecifics. Other attributes such as sex may influence rank acquisition and stability during group fusion events (Carter et al., 2013; Kohn, Meredith, Magdaleno, King, & West, 2015), particularly if one sex tends to be more aggressive or dominate the other (Tilson & Hamilton, 1984), or if there are sex differences in the costs of rank instability. For example, female chacma baboons, *Papio hamadryas ursinus*, exhibit elevated stress levels in response to female rank instability and the immigration of unfamiliar males (Engh et al., 2006)

Moreover, experimental studies have highlighted the role of 'coat-tail' effects, a process by which subordinates achieve high rank in the postfusion groups simply because of their prior familiarity with the postfusion dominant (Cristol, 1995; Wiley, 1990; Wiley, Steadman, Chadwick, & Wollerman, 1999). Coat-tail effects were initially proposed by Wiley (1990), as all individual dark-eyed juncos, *Junco hyemalis*, from one subgroup dominated all those from another subgroup following group fusion. Possible mechanisms generating coat-tail effects include the top-ranking individual showing preferential behaviours, such as foraging proximity, towards familiar subordinates or coordinated attacks by familiar individuals on unfamiliar individuals (Wiley, 1990; Wiley et al., 1999). However, the operation of coat-tail effects has received mixed support, with other studies providing no evidence that prior familiarity with a dominant facilitates the acquisition of higher ranks by subordinates in postfusion groups (Earley & Dugatkin, 2006; Wiley et al., 1999). It is possible that coat-tail effects (and other means of attaining high status via convention) become less significant if there are cognitive constraints or substantial differences in individual traits related to competitive ability (Smith & Parker, 1976). Therefore, in societies in which competitive attributes, such as relative body size, strongly predict social status, mechanisms such as coat-tail effects may operate less strongly.

Social organization and rank stability could be further modulated by alterations in environmental (and not just social) context, but this too is an understudied area (Silk et al., 2014). Understanding environmental impacts is important, because environmental parameters often fluctuate dramatically in space and time, and because any subsequent changes to individual behaviour can scale up to affect higher-order social structures, ultimately affecting population size, dynamics and persistence (Bull, Godfrey, & Gordon, 2012; Schaffner, Rebecchini, Ramos-Fernandez, Vick, & Aureli, 2012; Wong, 2012). In freshwater systems, alterations in water level can be a frequent occurrence and represent an environmental parameter that could cause changes in social organization (Sloman, Taylor, Metcalfe, & Gilmour, 2001; Sneddon, Hawkesworth, Braithwaite, & Yerbury, 2006; Stradmeyer, Höjesjö, Griffiths, Gilvear, & Armstrong, 2008). Flooding and drought occur regularly in these systems although the consequences for social behaviour are currently unclear (Ledger, Brown, Edwards, Milner, & Woodward, 2013). One mechanism by which reduced water depth could trigger changes in social organization is via the effective increase in local population density and hence encounter rates (Sneddon et al., 2006; Stradmeyer et al., 2008). A second potential mechanism is via a reduced access to key habitats at low water level, particularly habitats that may be located along the edge of a water body and particularly for benthic organisms (Fischer & Öhl, 2005). Yet despite research on the effects of water depth on the integrity of dominance relationships in response to fission–fusion, the underlying processes are unknown (Silk et al., 2014).

To address these knowledge gaps, we investigated the influence of water depth on the fusion dynamics of a social freshwater fish, the eastern mosquitofish, *Gambusia holbrooki*. This is a poecilid fish native to North America which has become highly invasive throughout the world, including Australia (Lloyd, Arthington, & Milton, 1986; Pyke, 2005; 2008). It is an appropriate model system for our investigation for several reasons. First, previous research has demonstrated that *G. holbrooki* is an aggressive yet social species (Burns, Herbert-Read, Morrell, & Ward, 2012; Lopez, Wong, & Davis, 2016; Matthews & Wong, 2015; Seebacher, Ward, & Wilson, 2013; Thompson, Hill, & Nico, 2012; Ward, 2012) that forms well-defined linear size-based hierarchies when kept in isolated groups (Matthews & Wong, 2015). Second, while these fish are known to tolerate a wide range of environmental conditions (Cherry, Rodgers, Cairns, Dickson, & Guthrie, 1976; Keup & Bayless, 1964), the fact that they inhabit ephemeral water bodies in often very dry environments (Pyke, 2005) means that they could be subject to alterations in water depth on a regular basis. Third, while there have been no attempts to quantify fission–fusion dynamics in the wild (unlike other poecilids; Croft et al., 2003; Croft, Krause, & James, 2004), the fact that they inhabit interconnected ponds, rivers and creeks means that a dynamic fission–fusion society is more characteristic of their social organization than the static, restricted membership groups seen in other social fishes (Wong & Buston, 2013).

Using. *G. holbrooki*, we experimentally investigated the process of group fusion under different water level regimes addressing the following key questions. (1) Is social organization influenced by group fusion and water depth? (2) Are levels of conflict influenced by group fusion and water depth? (3) Is the stability of rank relationships following fusion influenced by water depth? (4) Is postfusion rank influenced by coat-tail effects and water depth? In addition, we accounted for the effects of individual attributes, namely size and sex. We predicted that individuals would form size-based hierarchies that are robust to changes in social and environmental factors. Overall levels of conflict were expected to increase and rank stability decrease following group fusion and reduced water depth. Females were expected to exhibit increased conflict and decreased rank stability in response to group fusion and in reduced water depth. Finally, we predicted that coat-tail effects would not influence postfusion rank if size were a strong predictor of dominance. Our study therefore generates a more comprehensive understanding of interactions between altered social (fusion) and environmental (water depth) context on the structure and stability of dominance hierarchies.

METHODS

Collection and Housing

Gambusia holbrooki were collected between March and April 2015 from a freshwater creek at the University of Wollongong, NSW, Australia (34°24′S, 150°53′E). A total of 96 fish were used for the experimental trials. Fish were caught using a bait and net