



Sexual selection promotes colonial breeding in shell-brooding cichlid fish



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Colonial species breed in densely aggregated territories containing no resources other than nest sites. This behaviour is usually explained by natural selection, for instance through benefits resulting from reduced predation risk. An alternative hypothesis suggests that, as in lek breeding systems, sexual selection may be responsible for the aggregation of competitors, driven by an increased potential for female mate choice among closely assembled males. *Lamprologus callipterus*, a shell-brooding cichlid fish of Lake Tanganyika, provides an ideal test case for the utility of lek evolution models to explain colonial breeding, because breeding territories are established by males before pairing. Large males collect and defend empty snail shells that are then chosen by females for breeding. We checked for a potential influence of sexual selection on colonial breeding in *L. callipterus* by testing predictions of the hot-shot and female preference hypotheses of lek mating models. In the field, we found that territories of larger males were more centrally located and that females preferred to breed with males surrounded by many neighbours, two findings that are consistent with lek mating models. Female preference suggests that sexual selection affects colonial breeding in *L. callipterus*, which implies an influence of sexual selection on the evolution of colonial breeding at large.

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There is ongoing debate about why individuals breed in colonies (Danchin & Wagner, 1997; Höglund & Alatalo, 1995; Neff & Pitcher, 2008; Sachs, Hughes, Nuechterlein, & Buitron, 2007). In breeding colonies, individuals aggregate and defend nest sites or small territories that contain no other resources (Danchin & Wagner, 1997; Perrins & Birkhead, 1983; Siegel-Causey & Kharitonov, 1990; Wittenberger & Hunt, 1985). This breeding pattern is widespread in vertebrates ranging from fish (Gross & MacMillan, 1981; Tyler, 1995) to reptiles (Trillmich & Trillmich, 1984) and marine mammals (Terhune & Brilliant, 1996). Most prominently, this breeding pattern is prevalent in seabirds, in which 95% of all species breed in colonies (Brown, Stutchbury, & Walsh, 1990; Wittenberger & Hunt, 1985). Several evolutionary mechanisms have been proposed to explain colonial breeding. 'Conspecific models' assume that the fitness benefits of colonial breeding are gained from nesting near conspecifics (Sachs et al., 2007): nesting sites should be aggregated

if colonial breeding, for instance, increases foraging efficiency (Beauchamp, 1999), facilitates information transfer (Barta & Giraldeau, 2001; Buckley, 1997), reduces the predation risk for offspring (Gross & MacMillan, 1981; Picman, Pribil, & Andre, 2002; Post, 1998; Schaedelin, Fischer, & Wagner, 2012; Tyler, 1995) or enables parasitic reproduction (Picciulin, Verginella, Spoto, & Ferrero, 2004). 'Habitat models', on the other hand, assume that the fitness benefits of colonial breeding are gained through the characteristics or location of the colony site (Sachs et al., 2007), mainly when suitable breeding habitats are limited (Johnson & Walters, 2011; Kiester & Slatkin, 1974; Wittenberger & Hunt, 1985). Either way, these benefits must outweigh the potential costs of colonial breeding, such as increased parasite transmission, potential infanticide and competition for mates (Danchin & Wagner, 1997; Kiester & Slatkin, 1974).

In lek mating systems, in contrast, males aggregate at display arenas which females visit solely for the purpose of mating (Höglund & Alatalo, 1995; Kiester & Slatkin, 1974; Loiselle et al., 2007). Sexual selection is usually held responsible for the evolution of leks. First, the 'hot-shot model' assumes that certain males are preferred by females over other males, and that subordinate or less attractive males aggregate around such 'hot-shots' in order to increase their mating success (Bednekoff, 2002; Beehler & Foster,

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1988; Westcott & Smith, 1997). Second, the 'female preference model' assumes that females benefit from clumped male territories either because they can better estimate relative mate quality (Wagner, 1998) or because males of high quality tend to be found in larger aggregations (Höglund & Alatalo, 1995). According to this model, females preferentially settle in large aggregations (Fletcher & Miller, 2006). Third, the 'hot-spot model' (Bradbury, Gibson, & Tsai, 1986) hypothesizes that breeding aggregations are a result of males settling in regions with high female abundance (Höglund & Alatalo, 1995; Westcott, 1997). Females may have large overlapping home ranges relative to male territory size or well-defined travel routes (Bradbury et al., 1986; Westcott, 1997). Males aggregate to increase pairing success, and extrapair copulations (EPCs) may occur as a by-product of the aggregation (Fletcher & Miller, 2006). Finally, the 'kin selection model' assumes that subordinate males gain inclusive fitness benefits by aggregating among related males (Bradbury & Gibson, 1983; Kokko & Lindström, 1996). Only males that are related to the dominant male aggregate (Fletcher & Miller, 2006).

The hidden lek hypothesis of colonial breeding provides an alternative explanation, assuming that intersexual selection (female choice) may be responsible for the aggregation of competitors also in nonlekking species that engage in paternal care (Wagner, 1998). This hypothesis is an extension of the 'EPC hypothesis' (Wagner, 1993), which originated from the discovery that socially monogamous birds of both sexes may pursue EPCs (Birkhead & Møller, 1992). The hidden lek hypothesis assumes similar mechanisms to those in lekking species to be responsible for an aggregation of nests in a colony (Bradbury, 1981), such as the 'hot-shot', 'female preference' 'hot-spot' and 'kin selection' models (Fletcher & Miller, 2006). Five criteria are required for breeding colonies to classify as hidden leks (Fletcher & Miller, 2006), four of which focus on the role of extrapair matings for the accumulation of territories: (1) The species must be socially monogamous or polygynous, where females develop pair bonds with males that provide some form of paternal care; (2) territorial males aggregate, forming arenas where EPCs occur; (3) females seek EPCs and are able to select extrapair mates; extrapair males (4) provide no parental care and (5) do not monopolize resources required by females. A study of colony formation in the socially monogamous least flycatcher, *Empidonax minimus*, revealed that some predictions of the hidden lek hypothesis indeed apply in that species (Tarof, Ratcliffe, Kasumovic, & Boag, 2005).

The current consensus is that colonial and lek mating systems differ distinctively in the parental care system: lekking males provide no parental care while colonial males typically provide substantial and usually essential care. The role of sexual selection is assumed to be restricted to the evolution of leks and its importance is neglected as a driver of colonial breeding, because in many colonial species, breeding pairs choose a nest site together, i.e. after mate choice and pairing. However, if aggregated territories are founded by males only, there is high potential for sexual selection to operate. For example, in bluegill sunfish, *Lepomis macrochirus* (Gross & MacMillan, 1981), the cichlid *Lamprologus callipterus* (Sato, 1994), boat-tailed grackles, *Quiscalus major* (Post, 1998), Mediterranean damselfish, *Chromis chromis* (Picciulin et al., 2004), lesser kestrel, *Falco naumanni* (Calabuig, Ortego & Aparicio 2011) and western sandpipers, *Calidris mauri* (Johnson & Walters, 2011), males establish a territory first and females settle later. In all these cases, sexual selection mechanisms that are responsible for lek evolution might operate as well, but they have not been explicitly addressed. In boat-tailed grackles, for instance, the difference in reproductive success between colonial and solitary females is explained by the males' defence of colonies from predatory birds (Post, 1998). Breeding colonies of lesser kestrels apparently result

from neutral colony selection by first-year birds based on nest site availability (Calabuig et al., 2011). Bluegill sunfish colonies were assumed to result from reduced brood predation through nest aggregations (Gross & MacMillan, 1981), whereas in the Mediterranean damselfish, colonial nesting was shown to facilitate parasitic reproduction (Picciulin et al., 2004).

Lamprologus callipterus, a cichlid fish endemic to Lake Tanganyika, provides an ideal opportunity to explore predictions derived from lek evolution models to explain colonial breeding. Here, unlike in most colony breeders, males establish their aggregated territories first, i.e. before pairing. Therefore, a direct influence of females on colony formation at the time of territory establishment is very unlikely. Instead, males may be selected to aggregate prior to female arrivals in order to subsequently increase their mating success. Females choose males, established nests or shells contained therein for mating, which yields a high potential for female choice to operate after initial colony formation. The breeding system of *L. callipterus* seems to conform to a number of predictions from models of lek mating systems. Males defend territories in clusters (hereafter referred to as 'nest'), which contain no resources other than empty snail shells attracting females for mating (Mitchell, Wirtz Ocana, & Taborsky, 2014; Nakai, Yanagisawa, Sato, Niimura & Gashagaza 1990). However, in contrast to a pure lek, females stay in the male territory after mating, and males indirectly care for the brood by antipredator defence (Maan & Taborsky, 2008; Sato, 1994). Hence, the mating system of *L. callipterus* conforms also to resource defence polygyny (Emlen & Oring, 1977). Territories of bourgeois males consist of accumulated gastropod shells of the species *Neothauma tanganicense* or *Paramelania damoni*, which serve as exclusive breeding substrate for females (Gashagaza, Nakaya, & Sato, 1995; Sato, 1994; Sato & Gashagaza, 1997; Schütz & Taborsky, 2000). Shells are collected nearby, or stolen from neighbouring nests (Maan & Taborsky, 2008; Mitchell et al., 2014; Sato, 1994). Females perform brood care for 10 to 14 days within these shells (Sato, 1994).

Throughout the breeding area, sneaker males of all sizes try to steal fertilizations from territory owners (Sato, 1994; Schütz & Taborsky, 2000; Taborsky, 1998, 2001). Additionally, small dwarf males attempt to gain fertilizations by entering shells with a spawning female inside (Sato, Hirose, Taborsky, & Kimura, 2004; Taborsky, 1998, 2001) and releasing sperm from within the shells (Wirtz Ocana, Meidl, Bonfils, & Taborsky, 2014). Sneakers and dwarf males do not show any parental care (Taborsky, 2001), and most sneaker males are too small to claim breeding territories, because they cannot manage to carry shells (Schütz & Taborsky, 2005). In contrast to females breeding on hidden leks, which are expected to prefer aggregated males to improve the potential for EPCs (Tarof et al., 2005; Wagner, 1993), in *L. callipterus* females are not able to actively seek extrapair matings, since egg deposition and fertilization takes place inside the snail shell (Schütz, Heg-Bachar, Taborsky, & Heg, 2012; Taborsky, 2001). The only scope for female choice regarding parasitic males would occur after a female has already chosen a nest and entered a shell, i.e. during her spawning. A dwarf male attempting to enter a shell for spawning needs to pass the female, which can resist this attempt as this passing usually requires a slight backward movement of the female towards the shell entrance (Sato et al., 2004; D. Schütz, S. W. Ocana, M. E. Maan & M. Taborsky, personal observations).

In this study, we examined the influence of sexual selection on colonial breeding in *L. callipterus* by testing some predictions of lek mating models. In this species nesting males aggregate after a dispersal period extending well over a year (Schütz, Parker, Taborsky, & Sato, 2006), during which individuals mix and roam about in schools (Sato et al., 2004; Taborsky et al., n.d.), just as females do between successive broods (Schütz et al., 2006).

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