



Be a good loser: A theoretical model for subordinate decision-making on bi-directional sex change in harem fish



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ABSTRACT

Among animals living in groups with reproductive skew associated with a dominance hierarchy, subordinates may do best by using various alternative tactics. Sequential hermaphrodites or sex changers adopt a unique solution, that is, being the sex with weaker skew when they are small and subordinate, and changing sex when they become larger. In bi-directionally sex-changing fishes, although most are harem and basically protogynous, subordinate males can change sex to being females. We study a mathematical model to examine when and why such reversed sex change is more adaptive than dispersal to take over another harem. We attempt to examine previously proposed hypotheses that the risk of dispersal and low density favor reversed sex change, and to specify an optimal decision-making strategy for subordinates. As a result, while the size-dependent conditional strategy in which smaller males tend to change sex is predicted, even large males are predicted to change sex under low density and/or high risk of dispersal, supporting both previous hypotheses. The importance of spatiotemporal variation of social and ecological conditions is also suggested. We discuss a unified framework to understand hermaphroditic and gonochoristic societies.

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1. Introduction

Most animal societies are not egalitarian but show reproductive skew, i.e. unequal sharing of reproductive success, in favor of dominant individuals (Nonacs and Hager, 2011). This raises the question why subordinates remain in a group, rather than disperse to another location. Although this question was originally proposed and has been mainly studied with regard to cooperatively breeding species (Emlen, 1982; Brown, 1987; Wong and Balshine, 2011), the same question can be addressed in non-cooperatively breeding societies with a high reproductive skew (Gardner et al., 2003; Wong, 2010; Wong and Buston, 2013). Unlike helpers caring their kin, subordinates in non-cooperative breeders do not achieve indirect fitness benefits through kinship, and thus should have other ecological benefits, such as the benefit of philopatry (Gardner et al., 2003; Wong, 2010).

In contrast to gonochorists, which usually compete over reproductive status with same-sex individuals, hermaphrodites can adjust their sexual expression to their conditions including social

status (Wong et al., 2012). Socially determined sex change provides a good example of such adjustment. Functional sex change is a reproductive strategy adopted by a wide range of organisms (Policansky, 1982; Vega-Frutis et al., 2014). Theoretically, individuals should first mature as a sex with weaker size-based reproductive skew, and then change into a sex with stronger size-based skew after attaining size or dominance (Charnov, 1982). This model is referred to as the “size-advantage hypothesis” (Ghiselin, 1969) and is supported by numerous studies, especially on marine fishes (Warner, 1984; Charnov, 1982; Kuwamura and Nakashima, 1998; Munday et al., 2006). The timing of sex change is often controlled by social status in teleost fishes (Robertson 1972; Ross 1990). For example, in harem fish species in which a dominant male monopolizes all eggs produced by harem females, it is almost impossible for subordinates to reproduce as males. Hence, they should first mature as females and then change their sex into males when they grow and become dominant. In other words, harem mating systems usually favor protogynous sex change (Warner, 1984), and such change is associated with dominant status (Ross, 1990). In this case, subordinates can do best by being the sex with weaker skew. However, they sometimes adopt alternative tactics to heighten their social status, including dispersal (Sakai et al., 2001; Manabe et al., 2007b), growth acceleration (Sakai, 1997; Hamaguchi et al., 2002) and bachelor sex change, in which females

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change sex without disappearance of harem males and become bachelor males (Moyer and Zaiser, 1984; Aldenhoven, 1986; Iwasa, 1991; Sakai, 1997; Takamoto et al., 2003; Yamaguchi et al., 2013).

The most dynamic example of such interaction between sexuality and social status is bi-directional sex change among fishes (Kuwamura and Nakashima, 1998; Munday et al., 2006; Munday et al., 2010). This ability is known in more than 30 species (Kuwamura et al., 2016). Many of them are harem-polygynous (except for monogamous gobies and facultatively polygynandrous damselfish) and, as predicted by size-advantage hypothesis, basically protogynous (Munday et al., 2010). When two males accidentally cohabit, the smaller and subordinate one changes sex back to female (Sunobe and Nakazono, 1993; Kuwamura et al., 2002, 2011, 2014a, b; Sakai et al., 2003; Wittenrich and Munday, 2005; Manabe et al., 2007a; Sakurai et al., 2009; Kadota et al., 2012; but see Manabe et al., 2008). Although such reversed sex change seems adaptive as the best of a bad situation for subordinates (Kuwamura and Nakashima, 1998), alternative tactics are also possible. Subordinate males can remain as males by dispersal to take over a harem with a resident male smaller than themselves, or in which the male disappeared recently, or to wait for the recruitment of new females as bachelors (Kadota et al., 2012; Kuwamura et al., 2014a). Because harem males can achieve much higher fitness than females in polygynous species, such alternative tactics might be favored.

Two factors are hypothesized to facilitate reversed sex change. First, if the mortality risk associated with inter-group dispersal is high, dispersal may no longer be adaptive (Nakashima et al., 1996; Munday, 2002; Munday et al., 2010). The high risk of movement constrains dispersal, even if successful dispersal could be beneficial (Emlen, 1982). Reversed sex change by subordinates can evolve as an alternative to risky dispersal. Bi-directional sex change is relatively common in cryptic, symbiotic, and/or demersal fishes (Munday et al., 2010), such as the gobies of genera *Trimma* (Sunobe and Nakazono, 1993; Manabe et al., 2007a, 2008; Sakurai et al., 2009) and *Gobiodon* (Nakashima et al., 1996; Munday et al., 1998; Cole and Hoese, 2001; Munday, 2002). Since these fishes suffer from a high risk of predation when they are away from their habitats or hosts, it supports the risk-of-dispersal hypothesis. However, several non-cryptic and pelagic fishes in which the risk of dispersal is apparently small also conduct bi-directional sex change (Munday et al., 2010). These examples can be explained by a limited mate availability caused by low density (Kuwamura et al., 2011, 2014a, b), because reversed sex change can be experimentally induced by female removal in such fishes including *Labroides dimidiatus* and *Centropyge ferrugata* (Kuwamura et al., 2011). This can induce reversed sex change, not only by producing bachelor males (Kuwamura et al., 2002, 2011, 2014a, b), but also by reducing the benefit of harem males. Small harem size and low total fecundity caused by low density weaken the reproductive skew among males on average, and thus dispersal to be a dominant male becomes less advantageous.

Another unsolved problem regarding bi-directional sex change is conditional decision-making by subordinate or bachelor males. The status of dominant males provides high reproductive success in polygynous species, as noted above. Therefore, it is predicted that only males with less opportunity to become dominant choose to change sex, while males with larger opportunity will choose other options. In other words, decision-making about sex change should be conditional, not only on environmental factors, but also on the conditions of individuals. This prediction is supported by the observation that males often re-acquire females without sex change after mate loss (Kadota et al., 2012; Kuwamura et al., 2014a, 2016). However, the norm of such decision-making has not been studied empirically or theoretically. It is also unknown how such decision-making should interact with extrinsic

environmental conditions to form an optimal conditional strategy. Given the importance of sex change as a tactic to cope with reproductive skew based on social dominance (see above), understanding such decision-making should contribute to the understanding of coevolution between sexual plasticity and social structure among hermaphroditic species. In this study, we examine the effect of environmental factors and the patterns of decision-making by subordinates by using mathematical modeling, to understand the mode of social living based on sexual plasticity.

2. Model

For this study, we examined a basically protogynous and polygynous fish with a harem mating system. Protogynous sex change is assumed to be socially controlled in a manner that follows the “suppression model” (Ross, 1990). In other words, only the largest and most dominant individual in a group becomes a male and fertilizes all the eggs produced by the females. The total fecundity by resident females of a harem (R) is assumed as identical for all harems. When two males accidentally cohabit within a group, the smaller one becomes a subordinate. Subordinates must decide whether to change sex to female and remain in the group, or to disperse to another group, depending on the expected reproductive success associated with each tactic. If it becomes a female, its fecundity is $as - c$, where s is the body size, a is a coefficient representing size-fecundity relationship, and c is the fecundity cost of sex change. If it disperses, it dies with a probability d , or invades another harem chosen randomly and causes male cohabitation again. Below we call this probability of death caused by dispersal d as “risk of dispersal”.

First, we suppose a male invaded a harem with a single resident male and multiple females. The expected reproductive success of a male which just has invaded a randomly chosen harem is denoted by $V(x)$, where x is the body size of the invader. The body size of the resident male is denoted by y . Because invasion occurs at random, the probability distribution of y reflects the size distribution of harem males $D(y)$. Below we explain how the expected reproductive success of the invader male is calculated for all possible cases of invasion, which is summarized in Table 1 (see also Fig. 1 for graphical representations).

If the invader is larger than the resident (i.e. $x > y$), the invader takes over the harem. Then the resident becomes subordinate and chooses dispersal or sex change (Fig. 1a). Reproductive success of the invader is identical to the total fecundity of resident females (i.e. R) when the former resident male disperses, and to total fecundity of resident females plus fecundity of the former resident male (i.e. $R + ay - c$) when the former resident male changes sex. If the invader is smaller than the resident (i.e. $x < y$), the resident keeps his dominant (harem male) position. Then the invader becomes subordinate and chooses dispersal or sex change (Fig. 1b). When the invader disperses again and attempts to invade another harem, the reproductive success of the invader is $(1 - d)V(x)$, because the next invasion attempt gives the same expected success as the previous one if it does not die during dispersal. When the invader changes sex, the reproductive success is the fecundity as a female (i.e. $ax - c$).

The expected reproductive success (abbreviated to RS) of an invader male of size x , $V(x)$, is represented by a summation of two terms (corresponding to the winning and the losing cases) as follows:

$$V(x) = \sum_{x>y} D(y) \Delta y * (\text{RS when resident } (y) \text{ is smaller than invader } (x)) + \sum_{x<y} D(y) \Delta y * (\text{RS when resident } (y) \text{ is larger than invader } (x)) \quad (1)$$

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