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Kin-directed food sharing promotes lifetime natal philopatry of both sexes in a population of fish-eating killer whales, *Orcinus orca*

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The vast majority of social animals exhibit sex-biased dispersal as a strategy to reduce kin competition and avoid inbreeding. Piscivorous 'resident' killer whales, *Orcinus orca*, of the eastern North Pacific, however, are unusual in that both sexes remain philopatric throughout life, forming highly stable, multigeneration matrilines that are closed to immigration. We conducted a 12-year study documenting extensive cooperative prey sharing within these matrilines, and hypothesized that extreme natal philopatry in resident killer whales arose due to inclusive fitness benefits gained by provisioning maternal kin. We found that prey sharing was nonreciprocal, and even though whales routinely foraged in mixed associations containing multiple matrilines, prey sharing among individuals belonging to different matrilines was very infrequent. Furthermore, maternal relatedness was a significant predictor of the frequency of prey sharing between individuals, with close maternal kin sharing more often than distant relatives or nonkin. Adult females were much more likely to share prey than adult males or subadults, probably because they mainly provisioned their offspring. However, food sharing was not limited solely to maternal care; all age–sex classes engaged in this behaviour by sharing with close maternal relatives, such as siblings and mothers. We also investigated the frequency of prey sharing between mothers and their offspring as a function of offspring sex and age, and found that maternal food sharing with daughters declined after daughters reached reproductive maturity, which could help to explain matriline fission events. The evolution of kin-directed food sharing requires the ability to reliably discriminate kin, which resident killer whales likely achieve through social familiarity and vocal dialect recognition. We propose that lifetime philopatry of both sexes has been selectively favoured in this population due to the inclusive fitness benefits of kin-directed food sharing, a cooperative behaviour that may also inhibit dispersal by reducing resource competition among kin.

Philopatry, or an individual's fidelity to its natal geographical range and/or social unit, affects the kin composition of groups and has important consequences for the evolution of social behaviour in gregarious animals. Philopatry may be selectively favoured because dispersers risk higher mortality from predation (Alberts & Altmann, 1995; Van Vuren & Armitage, 1994), aggressive interactions with unfamiliar conspecifics (Boonstra, Krebs, Gaines, Johnson, & Craine, 1987; Isbell & Van Vuren, 1996; Packer, 1979), or exposure to novel parasites (Cockburn, Scott, & Scotts, 1985). It is also a beneficial strategy when resources occur predictably, as philopatric individuals are familiar with local foraging areas and typically achieve greater feeding success than naïve immigrants (Lawson Handley & Perrin, 2007).

Philopatry is also promoted when cooperation provides fitness benefits to nondispersers through kin selection (Greenwood, 1980, 1983; Hamilton, 1964; Lawson Handley & Perrin, 2007). By increasing the survival or fecundity of close relatives through behaviours such as cooperative foraging (e.g. Packer, Scheel, & Pusey, 1990), food sharing (e.g. Boesch, 1994), alloparenting (e.g. Clutton-Brock et al., 2001; Lee, 1987; Pusey & Packer, 1987), territorial or predator defence (e.g. Allaine, 2000; Packer et al., 1990; Sherman, 1977), or thermoregulation (e.g. Koprowski, 1996; Lutermann, Schmelting, Radespiel, Ehresmann, & Zimmermann, 2006; Radespiel, Juric, & Zimmermann, 2009), participants improve their inclusive fitness. This indirect fitness enhancement occurs

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because augmenting the reproductive success of kin increases the frequency with which shared alleles (possessed by both the helper and beneficiary through common descent) are passed to future generations (Frank, 2013; Hamilton, 1964; Hepper, 1986; West, Pen, & Griffin, 2002; West-Eberhard, 1975). More specifically, the fitness benefit that the altruist gains from helping is influenced by the beneficiary's reproductive value (i.e. relative future population contribution) and its genetic relatedness to the altruist, weighed against any fitness costs that the altruist accrues by performing the helping behaviour (Frank, 2013; Gardner, West, & Wild, 2011; Hamilton, 1970; Hepper, 1986).

Despite its advantages, philopatry also has fitness costs, and most social species exhibit some degree of dispersal as a result of this cost–benefit trade-off. For example, while philopatric individuals must compete with kin for resources such as food, mates and territories, dispersers are able to minimize the costs associated with such competition by seeking these resources elsewhere (Dobson, 1982; Greenwood, 1980; Lawson Handley & Perrin, 2007; Moore & Ali, 1984; Peacock, 1996). By competing with unrelated individuals rather than kin, a disperser acquires the full fitness benefits of propagating its genotype without reducing the success of shared genotypes belonging to closely related individuals (Frank, 1986, 2013). Additionally, when resources vary spatially or temporally, dispersal is favoured over philopatry because it provides access to new foraging areas when local resources are scarce (Bowler & Benton, 2005; Isbell, Cheney, & Seyfarth, 1990; Lawson Handley & Perrin, 2007; Lurz, Garson, & Wauters, 1997; McPeek & Holt, 1992). Arguably the most important driver of dispersal is the fact that philopatry usually increases the chances of mating with kin. This explains why dispersal is typically sex biased: one sex must disperse to reproduce because inbreeding would have detrimental impacts on the fitness of offspring (Caley, 1987; Clutton-Brock, 1989; Cockburn et al., 1985; Greenwood, 1980; Lawson Handley & Perrin, 2007; Packer, 1979; Pusey, 1987). Mammalian dispersal is generally male biased, whereas females are more likely to be philopatric (Greenwood, 1980). However, mammals usually display some degree of female dispersal (e.g. Kappeler, Wimmer, Zinner, & Tautz, 2002; Packer, 1979), and a complete absence of dispersal by one or both sexes is comparatively rare (Lawson Handley & Perrin, 2007).

Long-term philopatry of both sexes in social mammals is very uncommon, having been documented in only a few species, including the brown long-eared bat, *Plecotus auritus* (Burland, Barratt, Nichols, & Racey, 2001; Entwhistle, Racey, & Speakman, 2000; Park, Masters, & Altringham, 1998), the common bentwing bat, *Miniopterus shreibersii* (Rodrigues, Ramos Pereira, Rainho, & Palmeirim, 2010), the long-finned pilot whale, *Globicephala melas* (Amos, Schlotterer, & Tautz, 1993), and a piscivorous ecotype of 'resident' killer whale, *Orcinus orca* (Bigg, 1982; Ford, Ellis, & Balcomb, 2000). In the absence of permanent, sex-biased dispersal, these animals avoid inbreeding through a mating system known as natal group exogamy, in which males do not father the offspring of females within their own groups, but instead mate with unrelated females by visiting other groups or during temporary, multigroup associations (Amos et al., 1993; Amos, Barrett, & Dover, 1991; Andersen & Siegismund, 1994; Barrett-Lennard, 2000; Burland et al., 2001; Ford et al., 2011; Hoelzel et al., 2007; Pilot, Dahlheim, & Hoelzel, 2010; Rodrigues et al., 2010). For males, natal group exogamy eliminates the negative fitness consequences of philopatry (inbreeding and within-group competition for mates), so remaining with the natal group becomes advantageous for both sexes, not just females (Burland et al., 2001).

Even though food sharing and other forms of kin-directed cooperation are quite common among terrestrial mammals, no terrestrial species exhibit the extreme degree of natal philopatry (i.e. life-long maternal association by both sexes of offspring) that is displayed by resident killer whales and long-finned pilot whales. This raises the question of why this unusual strategy appears only to have evolved in certain toothed whales. Philopatry can only arise when the benefits of remaining in the natal group outweigh its costs, and group living may be generally less costly for cetaceans than for terrestrial mammals for several reasons. For one, the cost of locomotion is lower for cetaceans, and so they are able to travel continuously over greater distances (Connor, 2000). In addition, cetacean neonates are able to follow their mothers from birth, eliminating the need for reproductive females to remain at a specific breeding site (Connor, 2000). Both traits allow cetaceans to access more prey patches over larger home ranges at a lower cost of locomotion than terrestrial mammals, meaning that they can afford to live in larger groups without greatly increasing the level of feeding competition experienced by group members (Connor, 2000). Bats are another group of mammals known to display bisexual natal philopatry, probably because flying, while more costly than swimming, is still less costly than terrestrial locomotion (Tucker, 1970, 1975). Although bats are unlike cetaceans in that they are tied to colonial breeding sites, they are comparably mobile, which could explain why several bat species are highly philopatric without incurring excessive resource competition costs (Connor, 2000).

The social organization and genealogy of resident killer whales has been studied in detail since 1973 by using photo-identification of natural markings to conduct annual censuses of this population (Bigg, 1982; Ellis, Towers, & Ford, 2011; Ford et al., 2000; Towers, Ellis, & Ford, 2015). These studies have revealed that resident killer whales live in extremely stable matrilineal groups that are closed to immigration, and that both sexes remain philopatric throughout life (Ford et al., 2000; Parsons, Balcomb, Ford, & Durban, 2009). Cases of individuals dispersing from their natal matriline are exceedingly rare and likely anomalous. The few documented dispersal events include three orphans that became separated from their matrilines following the deaths of their mothers, and two lone, postreproductive matriarchs that were 'adopted' by closely related groups following the deaths of their own offspring. Although individual dispersal is almost nonexistent in this population, new social groups have arisen through a process of group fission along maternal lines (Bigg, Olesiuk, Ellis, Ford, & Balcomb, 1990; Stredulinsky, Ellis, & Ford, 2016).

Matrilines of resident killer whales that associate frequently with one another are known as pods (Bigg et al., 1990). These multimatriline groups are thought to share a common maternal ancestor, and although a pod's member matrilines can spend days or weeks apart, they associate more regularly than matrilines from different pods (Bigg et al., 1990; Ford, 2014). Matrilines belonging to the same pod also share similarities in their vocal repertoires (Ford, 1989). At their highest level of organization, resident killer whale populations are composed of acoustic clans, which share at least a portion of their vocal repertoire; whales from different clans have no calls in common (Ford, 1991). Paternity analysis has indicated that northern resident calves are rarely fathered by males from within their own pod or clan, and are never fathered by males from the same matriline (Barrett-Lennard, 2000). This system of natal group exogamy is reflected in the negative inbreeding coefficients (F_{is}) estimated for this population at both the pod (-0.112) and clan (-0.064) level (Barrett-Lennard, 2000). This is to say that members of the same pod or clan are more heterozygous than expected if mating occurred randomly. Thus, between-pod and between-clan differences in vocal behaviour are likely important social cues that guide mate choice and prevent inbreeding (Barrett-Lennard, 2000). Despite their tendency to outbreed, northern residents from the same clan or pod are more genetically similar than those