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Conspecific tolerance in a solitary small carnivore, the Pacific marten

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Abstract.—Holarctic martens (genus *Martes*) are small carnivores that are considered functionally solitary, with both resource scarcity and martens' inability to store energetic reserves posited as precluding social behavior. Interactions between martens are expected to be largely agonistic with the exception of mating and rearing of kits by adult females. Nonetheless, we documented multiple instances of conspecific tolerance by Pacific martens (*M. caurina*) during long-term monitoring of radio-marked animals in 2 study populations. Observations from radio-tracking and remotely triggered camera trap photographs suggested that pairs of martens traveled, foraged, and rested together. Presumed marten associations occurred both inter- and intrasexually and often, but not exclusively, consisted of younger (i.e., juvenile and subadult) individuals. Although social interactions between martens appeared to be highly uncommon, our work nonetheless supports mounting evidence that carnivore social systems are more nuanced than presumed. We briefly explore mechanisms that could allow for plasticity in marten sociality and offer suggestions on how future efforts can continue to elucidate behavioral phenomena that may be rare and difficult to document.

Resumen.—Las martas holárticas (género *Martes*) son pequeños carnívoros considerados funcionalmente solitarios, y se postula que la escasez de recursos y la incapacidad de almacenar reservas energéticas impiden su comportamiento social. Se espera que las interacciones entre martas sean en gran medida agonísticas, con la excepción del apareamiento y cuidado de las crías por parte de las hembras adultas. No obstante, hemos documentado múltiples casos de tolerancia conespecífica por parte de martas del Pacífico (*M. caurina*) durante el monitoreo a largo plazo de animales marcados por radio en dos poblaciones de estudio. Las observaciones realizadas a partir del monitoreo por radio y de fotografías tomadas con cámaras trampa disparadas a distancia, sugieren que las parejas de martas viajaban, buscaban comida y descansaban juntas. Las presuntas asociaciones de martas se produjeron tanto intersexualmente como intrasexualmente y a menudo, aunque no exclusivamente, estaban formadas por individuos jóvenes (i.e., juveniles y subadultos). Aunque las interacciones sociales entre martas parecen poco frecuentes, nuestro trabajo apoya la creciente evidencia de que los sistemas sociales de los carnívoros tienen más matices de lo que se presume. En este trabajo, exploramos brevemente los mecanismos que podrían permitir la plasticidad en el comportamiento social de la marta y ofrecemos sugerencias sobre cómo futuros esfuerzos pueden continuar para dilucidar fenómenos de comportamiento que pueden ser raros y difíciles de documentar.

Terrestrial mammalian carnivores are an ecologically important taxon that can structure and stabilize trophic systems (Ripple et al. 2014). Carnivore social systems have been of broad interest to ecologists (Macdonald 1983, Bekoff et al. 1984, Gittleman 1989), as they often parallel those of humans and can provide powerful insights into our own behavior (Schaller and Lowther 1969). Social organization of carnivorans varies considerably, but only a small proportion of carnivore species live in groups (Bekoff et al. 1984). Group-living arises when the advantages of tolerance outweigh the costs of competitive interactions between conspecifics (Carr and Macdonald 1986, Lindström 1986), and benefits of group living (e.g., cooperative hunting, coordinated territorial defense, shared parenting of offspring) are often readily apparent in social carnivores (Macdonald 1983, Gittleman 1989). Conversely, an inability to share limited resources is thought to be a primary mechanism driving carnivore solitariness (Carr and Macdonald 1986). Conspecific interactions of solitary carnivore species are expected to be infrequent and largely agonistic, other than a few obligatory exceptions (e.g., courtship or copulation; Sandell 1989, Creel and Macdonald 1995).

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Holarctic martens (American marten [*Martes americana*], European pine marten [*M. martes*], Japanese marten [*M. melampus*], Pacific marten [*M. caurina*], sable [*M. zibellina*], and stone marten [*M. foina*]; Anderson 1970, Stone and Cook 2002) are small carnivores that have been widely described as solitary (Powell 1979, Balharry 1993, Newman et al. 2011). Martens have large home ranges with little overlap among individuals, particularly within sexes (Buskirk and McDonald 1989, Moriarty et al. 2017). Relatively exclusive use of space by martens has been posited in part as a means to maintain individual food security (Powell 1979), as martens inhabit seasonally cold and snowy environments characterized by relatively low productivity (Zhou et al. 2011), where populations of primary prey may be seasonally or periodically scarce (Thompson and Colgan 1987). Their long, lean body profile incurs high metabolic rates and precludes accumulation of substantial fat deposits (Buskirk and Harlow 1989, Gilbert et al. 2009, Martin et al. 2020); thus, needing to meet high energetic requirements despite uncertain food availability makes it unlikely that martens can share resources or take part in social behaviors (e.g., Erlinge 1974). Accordingly, martens are believed to be intolerant of conspecifics (Newman et al. 2011) aside from female–male interactions during mating (approximately July–August; Lodé 1991, Ruggiero and Henry 1993, Tatara 1994) and female–offspring interactions during kit rearing (approximately April–September; Kleef and Tydeman 2009, Delheimer et al. 2021).

Here, we describe behaviors indicative of conspecific tolerance by Pacific martens in 2 populations in northern California (Fig. 1a) that contrast the assumption that Holarctic martens are strictly solitary. Presumed associations between martens involved at least 1 known individual (i.e., radio-marked, with sex and age confirmed by live capture), although both individuals were known in most instances, and all observations were documented via radio-tracking or photographs from remotely triggered camera traps. Our clearest evidence of conspecific tolerance consisted of an association between 2 male martens of different ages (M06, juvenile; M07A, yearling). The association between M06 and M07A was the most frequently observed, was the only interaction documented via both radio-tracking and photographs, and occurred over a relatively long time period (approximately 4 months). M06 and M07A were photographed together on 4 occasions between 14 January 2010 and 10 February 2010 (e.g., Fig. 1b). They were identified resting together via radio-tracking on 7 April 2010 and were also tracked to within close proximity (<100 m apart) on at least 4 occasions during the interval when other observations were documented (mid-January to early April).

Other marten associations were documented via radio-tracking or photographs alone, were observed on fewer occasions, and/or occurred over shorter time periods. Using radio-tracking, we identified 2 other instances of martens sharing rest sites, including a juvenile female (F19) and an adult male (M41) on 26 March 2016 and a yearling male (M39) and M41 on 24 May 2016. Similarly, 2 other pairs of martens were photographed together: 2 juvenile males (M01, M07B) on 3 occasions between 5 November and 21 November 2013 (e.g., Fig. 1c) and an adult female (F20) and an unknown marten on 6 occasions between 2 November and 22 November 2018 (e.g., Fig. 1d). Additional observations were less apparent instances of tolerance but still suggested associations between marten conspecifics. In particular, a juvenile female (F16) and a juvenile male (M38) were captured and radio-marked on the same day in traps placed next to each other; they were radio-tracked to proximal locations on at least 5 occasions and appeared to use some rest sites sequentially over a period spanning approximately 5 months (mid-April to mid-August). The latter observation, when 2 different martens used the same rest site but did not concurrently share it, occurred at more than 20 different rest sites. At least 10 individual martens exhibited this behavior and it predominantly involved adults of opposite sexes (e.g., a male using a rest site previously occupied by a female).

Although it is possible that earlier observations of conspecific tolerance by martens were regarded as anecdotal and went unreported, nuances of marten sociality may simply have been overlooked in previous studies because marten behavior is particularly difficult to witness directly (Allen et al. 2018, Delheimer et al. 2021). Conversely, it is relatively easy to infer intolerance of conspecifics by martens from avoidance (e.g., low home range overlap; Buskirk and McDonald 1989, Moriarty et al. 2017) or agonism (e.g., fighting or intraspecific killing; Hodgman et al. 1997, Bull and Heater 2001a, Spriggs et

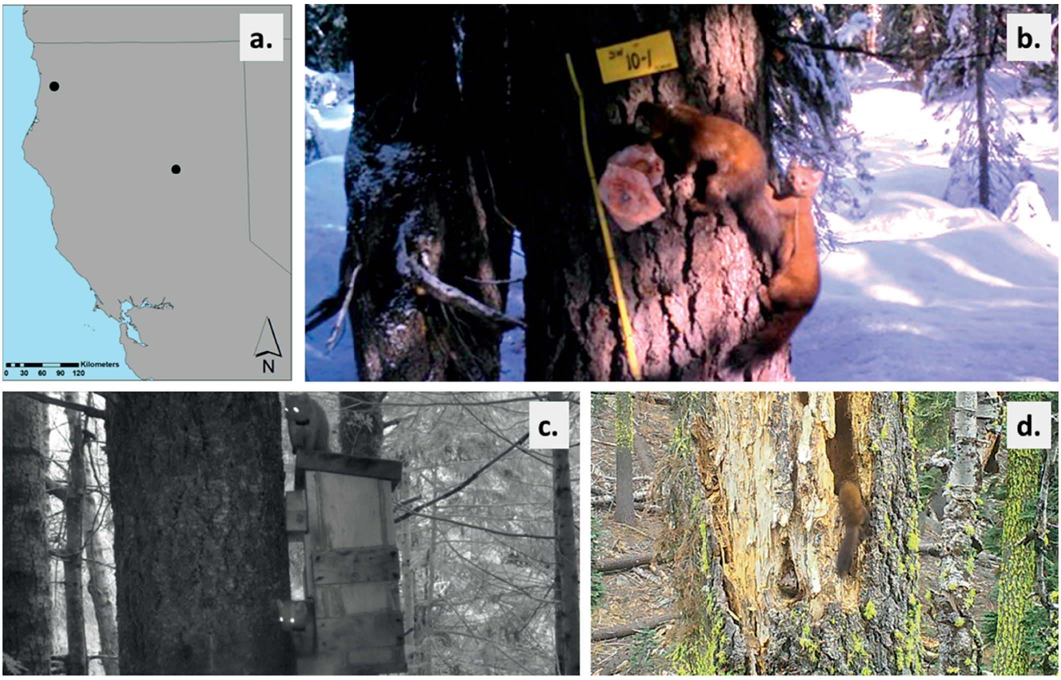

Fig. 1. ***a*,** Location of 2 Pacific marten (*Martes caurina*) study populations in northern California; ***b*,** M06 and M07A at a camera trap; ***c*,** M01 and M07B at an artificial cavity (see Delheimer et al. 2018); and ***d*,** F20 and an unknown individual at a rest site. These images represent examples from larger photographic series of each observation (typically tens to hundreds of images) that allowed us to confirm interactions as non-agonistic.

al. 2018). Nonetheless, we do not suggest that tolerant interactions among martens are common. Indeed, it is much more likely that conspecific tolerance by martens is rare and only occurs under certain circumstances. Our results instead reflect the remarkable amount of effort required to document cryptic behaviors that are presumably uncommon. Our research occurred over the span of a decade, included multiple studies, and required tens of thousands of human hours. The small number of observations described here emerged from the tracking of >75 individual martens, identification of >500 rest sites, collection of >2000 telemetry locations, and examination of >3 million photos.

Our work adds to a growing body of studies describing unexpected or atypical "social" behaviors by otherwise solitary carnivores. A seminal and well-described example is the congregation of brown bears (*Ursus arctos*) at salmon-bearing streams in Alaska, where interactions can range from group feeding to a variety of nonagonistic encounters between individual bears (e.g., mock fighting; Egbert and Stokes 1976). More recent evidence has been presented for species, like martens, whose behaviors are relatively cryptic. For instance, some adult male wolverines (*Gulo gulo*) appear to provide paternal care to both their female and male offspring (Copeland et al. 2017). Social play, cooperative foraging, and extensive cotraveling between adult jaguars (*Panthera onca*) have been observed in a high-density population in Brazil (Eriksson et al. 2022). Male fossas (*Cryptoprocta ferox*) in Madagascar can form pairwise associations that span multiple years and may be permanent (Lührs and Kappeler 2013). Elsewhere within the *Martes* genus, yellow-throated martens (*M. flavigula*) inhabiting tropical areas of India and South Korea have been documented hunting in pairs (Twining and Mills 2021) and foraging in groups of up to 6 individuals (Woo et al. 2015).

Tolerance of conspecifics in carnivores that are typically solitary may be more likely when resources are overabundant (e.g., at the carcass of a relatively large animal), when individuals can or must share space (e.g., males that overlap territories with multiple females to secure mating opportunities), or when animals are related (Macdonald 1983). Winter is characterized by food scarcity rather than abundance for Holarctic martens; for instance, martens in California commonly consume hibernating species (e.g., ground squirrels) and other items (e.g., migrating birds, berries) that are seasonally unavailable (Zielinski et al. 1983, Slauson and Zielinski 2017, 2019). Given that most of our observations occurred in the winter, it is unlikely that marten associations were a response to resource pulses. We posit that age and/or relatedness were more probable factors influencing conspecific tolerance in our study populations; for instance, we suspected that some observations (e.g., M01 and M07B, F16 and M38) involved siblings from juvenile cohorts. Both juvenile and yearling martens do not necessarily maintain home ranges (e.g., Bull and Heater 2001b); thus, young animals are potentially freed to pursue uncharacteristic arrangements (e.g., cotraveling or foraging). Avoiding conflict with other martens, particularly with related individuals, may confer genetic advantages as predicted by kin selection and inclusive fitness theories (Hamilton 1964).

Emerging and improving techniques may yield unique insights into cryptic behaviors, interactions, and drivers of sociality in otherwise solitary carnivore species. For instance, camera traps are increasingly being used to elucidate poorly understood phenomena (e.g., foraging, mating, predation) for many taxa (e.g., Linnell and Lesmeister 2020, Avrin et al. 2021, Zhu et al. 2022) and provided invaluable sources of evidence to support other observations in our work. Conducting systematic, long-term monitoring of marten rest sites via camera trap arrays could clarify their function and importance in marten social ecology, as rest sites are essential components of individual marten life histories (e.g., Taylor and Buskirk 1994, Wilbert et al. 2000) but also appear to play a role in interactions between martens (Zalewski 1997, Joyce 2013). Radio collars fitted with proximity loggers can reveal patterns of contact between individuals (Cross et al. 2012, Wilmers et al. 2015) by exchanging data during animal encounters including individual identification, temporal information (e.g., time, date, duration, frequency), and geographic location (Böhm et al. 2009, Ralls et al. 2013, Thiemer et al. 2016). Logger settings can be adjusted to ensure that exchanges only occur when animals are within short contact distances (e.g., <1 m), greatly increasing the likelihood that individuals are interacting rather than being proximal by chance (Ossi et al. 2022). Better documentation of rare and potentially complex behaviors can strengthen ecological inferences that can be made from encounters between individuals (Hertel et al. 2020).

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