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Cooperative hunting in the yellow-throated marten (Martes flavigula): Evidence for the not-so-solitary marten?

JOSHUA P. TWINING1,† and CHRIS MILLS2

1School of Biological Sciences, Queen’s University, 19 Chlorine Gardens, Belfast BT9 5DL UK
2Norfolk Birding, Yew Tree Cottage, Foxley Road, Thelnethorpe, Norfolk NR20 5PU UK

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Abstract. Species socio-ecologies are a key determinant of their ecological niche, and although dynamic, linked to environmental stochasticity, availability of resources, and inter- and intraspecific competition, socio-ecological theory under its prevailing framework inadequately captures the transient nature of this multi-faceted spectrum. Cooperative foraging is an example of an advanced social behavior that functions to release species from physiological and competitive limitations and is thought to only be observed in social species. Despite the advantages of social behaviors such as cooperative foraging, some groups, for example, the mustelids, are considered to be evolutionarily constrained in terms of sociality. The martens (Martes sp.) have been used as examples of obligately solitary species, physiologically and morphologically restricted by their inability to store fat and specialization in homogeneously distributed small vertebrate prey, and therefore presumed incapable of advanced social behaviors. Here, we provide evidence of cooperative foraging in the yellow-throated marten (Martes flavigula) in Ramanagar, India. We highlight that a tropical climate and a change in resource distribution through seasonal frugivory may release the species from typical constraints associated with martens, and other small carnivores. We argue that alongside a growing number of observations of social behaviors in solitary carnivores, our current framework for viewing socio-ecologies may limit our understanding of these species. Advances in biologging technologies are producing new data and insights into the social complexities of wildlife that will continue to challenge the expectations our current framework and these emerging data should be used as a platform to test and refine ecological theory regarding sociality and its drivers in animal populations.

Key words: animal behavior; cooperative foraging; martens; mustelids; small carnivore; social behaviors; sociality; socio-ecology.

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† E-mail: joshuaptwining@gmail.com

Resource distribution, physiological constraints, and intra- and interspecific competition are key drivers in the evolution of organisms’ observed socio-ecologies, and thus the ecological niches of species (Macdonald 1983, Svanback and Bolnick 2007, Macdonald and Johnson 2015). These pressures exist at all trophic levels, however, may be mitigated at higher trophic levels by the adoption of novel, cooperative foraging strategies that alter what, and how, resources can be obtained (Schoener 1974). Cooperative foraging may function to release species from physiological and competitive constraints, allowing species to overpower significantly larger, or otherwise difficult to subdue, energetically valuable prey which is otherwise unavailable to
individual foragers. For example, canids are evolved for fleet-footed predation, and thus suffer from a thermoregulatory ceiling, constraining maximum body size (Macdonald and Newman 2017). The largest extant canid, the gray wolf (*Canis lupus*, 50–80 kg), overcomes this thermo-dynamic conundrum through cooperative foraging strategies allowing the predation of ungulates up to an order of magnitude larger than an individual wolf (e.g., moose, *Alces alces*, 200–700 kg, Schmidt and Mech 1997). Such foraging strategies release predators from usual limits of body mass-to-prey size ratio, thereby increasing dietary niche (Kruuk 1972), and altering the availability and distribution of resources (Macdonald and Johnson 2015). Group hunting can also increase capture rates (Creel and Creel 1995) and buffer groups from starvation by limiting variation in capture, and individual consumption rates (Wenzel and Pickering 1991).

Despite its advantages, almost ubiquitous commonality through most taxa, sociality, and specifically cooperative foraging are rarely observed in the most taxonomically, and eco-morphologically diverse of carnivore groups, the mustelids (Macdonald and Newman 2017). Mustelid sociality is thought to be limited by their evolutionary morphology specialized for accessing arboreal and subterranean ecotones enabling the capture small vertebrate prey, which are theoretically homogeneously dispersed throughout the environment (Noonan et al. 2015). These morphological handcuffs resulting in a tendency toward territoriality are compounded by the biochemical pleiotropy of oxytocin inhabitation, necessary for delayed implantation observed in most mustelids, to the apparent detriment of affectionate predispositions (Caldwell et al. 2008). Within the mustelids, martens (*Martes* sp.) are used as an example of being physiologically restricted in terms of sociality (Newman et al. 2011). Larger, bulkier mustelids, for example, European badgers (*Meles meles*), are capable of storing large quantities of body fat. These energy reserves predispose more rotund species to be able to tolerate restricted food security, as stored fat can be used to survive periods of scarcity. Additionally, these larger species typically display behavioral advantages such as more complex subterranean dens, and the ability to enter torpor. Martens, on the other hand, must maintain a lean, elongate body type throughout their lives due to their arboreal and subnivean locomotive modes, ensuring effective hunting and predator avoidance capabilities (Harlow 1994, Nieminen et al. 2007). These life-history factors are underpinned physiologically in martens by an inability to store significant quantities of body fat. It has been suggested that these differences prevent martens from tolerating restricted food security, and therefore precludes them from precursive aggregation, which is the fundamental prerequisite to the formation of any social groups or behaviors (Newman et al. 2011). Martens have therefore generally been concluded to be obligately solitary (Powell 1979, Buskirk et al. 1994, Źalewski and Jedrzejewski 2006, O’Mahony et al. 2014) and prohibited from displaying advanced social behaviors. Despite badgers home range overlap and communal denning behavior, they are still considered to be solitary. This is because all animals interact in some context, for example, reproduction, so social grouping is not a contradiction of a solitary lifestyle per se (Leyhausen 1965). A key distinction between solitary and social being that solitary refers to animals where there is no collaboration between members in feeding, territory defense, or offspring rearing (Sandell 1989). Here, we report on an opportunistic observation of distinctly social behaviors of cooperative foraging in wild yellow-throated martens (*Martes flavigula*) in Ramnagar, India. The yellow-throated marten is the largest of the true martens (genus *Martes*) and occurs over a wide range from the Himalayas to eastern Russia, and south to the Sunda shelf in the Indo-Malay Archipelago (Proulx et al. 2004).

On the 5 December 2017, at approximately 8:00 am local time, the coauthor (C.M.) was traveling by vehicle on the Sambar road in the Corbett National Park. A lone adult Rhesus macaque (*Macaca mulatta*) was encountered in the middle of the track. A single yellow-throated marten appeared from the scrub and commenced stalking the macaque, almost immediately followed by a second yellow-throated marten of similar size. The martens were observed to alternately attempt to subdue the macaque over a 15-min period. The macaque remained bipedal and defended itself from the two predators (Fig. 1). Following this, the yellow-throated martens
attacked simultaneously. Able to overpower the macaque together (see Fig. 2), the martens held the macaque on the ground with one marten inflicting bite wounds to the rear leg, while the other appeared to deliver the decisive wound to the neck of the grounded macaque. The martens retreated and sat approximately 2 feet away from the subdued macaque; however, the macaque appearing revived, again stood up, resulting in further joint assaults by the pair of martens. After a few more minutes, with both martens attacking the would-be prey at once, the fatal bite was delivered to the spinal cord of the macaque. The martens were then observed to drag the carcass into the adjacent scrub out of view of the observers (Fig. 3).

Although yellow-throated martens have anecdotally been reported to hunt in pairs and threes, and these pairings have mused to be life-long (Lekagul and McNeely 1977, Sathyakumar 1999), there remains a complete paucity of published observations and research demonstrating cooperative foraging in yellow-throated martens, with only a handful of field studies on the species (Grassman et al. 2005, Woo et al. 2015, 2017). Compared to the wealth of literature on the six marten species inhabiting the Palaearctic (Balharry 1993, Powell 1979, Buskirk and McDonald 1989, Buskirk et al. 1994, Zalewski 1997, Zalewski et al. 2004, Caryl et al. 2012a, O’Mahony et al. 2014), this reiterates a knowledge gap in need of address on the most phylogenetically distinct of the Martes genus (Grassman et al. 2005, Koepflı et al. 2008).

Yellow-throated marten diet has been reported to be highly varied, composed of rodents, birds, fruits, and small ungulates (Zhou et al. 2011). The species tendency toward opportunistic frugivory changes the typical dispersion of resources from theoretically homogeneous to patchily distributed compared with a small mammal dominated diet observed in the Palaearctic martens (Balharry 1993, Zielinski and Duncan 2004, Caryl et al. 2012b). Patchily distributed resources may enable a greater level of tolerance toward conspecifics, acting as a precursor to the formation of social groups and more advanced social behaviors (Johnson et al. 2002). The lack of distinct seasonality as observed in the tropical regions inhabited by the yellow-throated marten, compared to the boreal martens which undergo prolonged periods of winter and resource scarcity, may also act to release them from the typical constraints against conspecific tolerance observed within most martens globally (Newman et al. 2011). If a tropical distribution does release species from certain
constraints of group living, this would have important implications for not only other members of the *Martes* genus, but also animal populations globally. Here, we provide evidence of a marten predating on a primate species and using cooperative hunting tactics to subdue its significantly larger prey. The hitherto lack of such observations may be representative of the difficulties of...
observing natural behavior in a cryptic and highly mobile species like the yellow-throated marten as opposed to rarity of the behavior in the species.

The relationship between the two individuals observed here is equivocal, and it is unknown whether the pair was a sibling coalition, parent–offspring, or a breeding pair, but despite this paucity of information, this observation is in opposition to martens being strictly solitary (Powell 1979). The observations described here are not the first to challenge the perhaps overly absolute conclusion that martens are physiologically constrained against social behaviors (Newman et al. 2011). There is emerging evidence of social complexity within the group and its close relatives, with observations of carcass sharing, paternal philopatry, and sibling coalitions in stone martens (Martes foina, Genovesi et al. 1997), European pine martens (Martes martes), and wolverines (Gulo gulo, Copeland et al. 2017).

As biologging technologies (e.g., camera traps, animal-borne sensors) allow us greater insight into the secret lives of wild animals, we are likely to uncover more nebulous socio-ecologies than our contemporary framework anticipates (Graw et al. 2019). Emerging data from such novel methods will enable analyses on the effects of group size and foraging strategies on prey size and capture rates and result in key theoretical advancements in our understanding of the evolutionary basis for social grouping and advanced social behaviors such as cooperative foraging. The growing number of observations of social behaviors in solitary species highlights the need for an updated, plastic, context-dependent framework, to better understand the various socio-ecologies observed within species in real-world systems. Martens and their close relatives shared physiological and morphological attributes that are thought to constrain them in regard to social grouping make them a particularly useful model system to test existing theory, and using emerging examples of advanced social behaviors and atypical grouping in these species, test, and update our concepts regarding the drivers of evolution of social behaviors in wild animal populations.

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