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Use of genetics to investigate socially learned foraging behavior in free-ranging black bears

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Investigating social learning in free-ranging mammals is gaining popularity among researchers. Natural experiments are ideal for studying social learning, but are rare compared to captive studies because of practical limitations and ethical concerns. Such experiments are often restricted or forbidden because they require manipulation of the environment, ecology, or behavior of free-ranging species. As a result, developing new methods to investigate social learning in the field is essential. The main goal of this study was to use genetic data and a new testing framework to determine if social learning from mothers to their offspring is at least partly responsible for free-ranging black bears foraging on human foods in Yosemite National Park. I estimated a relatedness coefficient and the most probable relationship for all combinations of 2 bears ($n = 150$) sampled in 2004–2007. I then grouped these pairs by their foraging behavior to test predictions deduced from asocial learning, transmission, genetic inheritance, and social learning hypotheses. Results from both analyses suggest that mother–offspring social learning is the primary mechanism responsible for black bears foraging on human food in Yosemite. In addition, results also suggest that some bears are innovators, learning to forage on human food as independents. I found no support for the genetic inheritance hypothesis.

Key words: asocial learning, black bear, conditioning, foraging behavior, genetic inheritance, microsatellite, relatedness, social learning, *Ursus americanus*, Yosemite National Park

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Animal behaviors are genetically inherited (Arnold 1981), acquired from the environment via learning (Heyes 1994; Heyes and Galef 1996; Box and Gibson 1999; Galef and Whiskin 2001), or shaped by the interplay of genes and learning (Kandel et al. 2000). Learning involves complex ontogenetic processes that allow animals to acquire, store, and then use information about their environment (including other animals—Galef and Laland 2005). Animals can learn asocially and socially (Heyes 1994; Galef and Whiskin 2001). Asocial learning occurs when animals learn via independent trial and error, and social learning occurs when animals learn by observing or interacting with conspecifics or the products of their behavior (Laland et al. 1993; Heyes 1994; Galef and Laland 2005). Social learning can enable animals to acquire information relevant to many biologically important activities such as choosing a mate, avoiding predators, and foraging (Kendal et al. 2010). Many species have evolved an ability to use information provided by others, such as parents, to guide learning (Galef and Laland 2005). Adopting the use of such socially acquired information potentially allows naïve animals, such as juveniles, to gain fitness advantages by circumventing the process of trial and error (Laland 2004; Galef and Laland 2005).

Social learning has been studied extensively in birds, fish, primates, rodents, and other mammals in controlled environments (Galef and Giraldeau 2001), but to date little research has been conducted on free-ranging animals (Lonsdorf and Bonnie 2010; Reader and Biro 2010; Thornton and Raihani 2010). In general, social learning is poorly understood in free-ranging animals because of the inherent difficulties associated with observing animals or controlling their experiences in noncaptive settings. For this reason, developing new approaches to investigate social learning in animals in noncaptive settings is important (Galef 2004; Franz and Nunn 2009; Kendal et al. 2009).

Researchers primarily use ethnographic approaches or manipulative "natural" experiments to study social learning in free-ranging animals (Lonsdorf and Bonnie 2010; Reader and Biro 2010). The ethnographic approach uses observational data from long-term field studies to infer social learning as the mechanism responsible for differences among social groups when genetic or ecological explanations seem unlikely (e.g., Whiten et al. 1999; Rendell and Whitehead 2001; Perry et al. 2003). Some manipulative natural experiments attempt to control for these confounding factors by seeding groups of animals with different behaviors and documenting transmission, or by translocating groups from one place to another and documenting any changes in their behavior (e.g., Helfman and Shultz 1984; Warner 1988; Lonsdorf and Bonnie 2010). Although using experimental methods in noncaptive settings is becoming more commonplace in the field of social learning, such studies are still rare compared to captive studies (Reader and Biro 2010) because of practical limitations and ethical concerns (Cuthill 1991; Putman 1995). In particular, experimental studies are often restricted or forbidden in many areas such as national parks because they require manipulation of the environment, ecology, or behavior of animals. As a result, there is need to develop new methods to investigate social learning in model free-ranging species (Lonsdorf and Bonnie 2010; Donaldson et al. 2012).

Black bears (*Ursus americanus*) can be used as a model species for studying social learning in free-ranging animals because, like other animals with large brains, black bears have good memory, curiosity, and behavioral plasticity (Gittleman 1986; Gilbert 1999). In addition, black bears spend between 16 and 18 months with their mothers, yet are primarily solitary as independents (Pelton 2003). Unlike more social species that live in extended family groups, these 2 distinct periods in life history provide researchers with an opportunity to investigate the vertical transmission of behavior from mother to offspring. If social learning occurs among black bears, then this form of learning likely happens most frequently during the period when a cub is dependent on its mother. By contrast, asocial learning would likely occur once bears achieve independence from the juvenile (yearling–subadult) stage onward.

Black bears also can be considered a model species in which to study the transmission of foraging behavior in free-ranging animals (especially those with prolonged mother–offspring relationships) because bears can be classified into 1 of 2 foraging classes: those that forage on human-derived foods (hereafter, human foods) and those that do not. Generally, if independent offspring have similar foraging behavior to that of their mothers when these mothers reared these offspring as cubs (Mazur and Seher 2008), then this behavior could have been transmitted via genes or social learning, or combination of mechanisms. If independent offspring did not forage on human food when reared, but forage on human foods as independents, then these bears likely learned this behavior via asocial learning.

Two recent studies investigated the transmission of foraging behavior from parent to offspring by monitoring black bears. Mazur and Seher (2008) tracked the foraging behavior of female black bears and their offspring in developed areas (i.e., areas with high human use such as campgrounds) in Yosemite and Sequoia National Parks, California, until offspring were 2 years old. They concluded that the foraging behavior of yearlings was strongly related to their rearing conditions as cubs (Mazur and Seher 2008). They found that cubs were 45 times more likely to forage on human foods as yearlings if their mothers reared them in developed areas. Conversely, they found that cubs would likely forage on nonhuman foods (hereafter, natural foods) as yearlings if their mother reared them in undeveloped areas (Mazur and Seher 2008). Breck et al. (2008) also investigated foraging behavior in black bears using both genetic and behavioral data for bears captured and tracked via telemetry in Yosemite National Park (hereafter, Yosemite) in 2001–2002 (Matthews et al. 2006) and in the Lake Tahoe Basin and Carson Front, California, in 1997–2002 (Beckmann and Berger 2003). Breck et al. (2008) concluded that behavior of foraging on human foods was not solely a function of social learning or inheritance because they found little evidence suggesting that foraging behavior partitioned along related lineages (Breck et al. 2008).

The 2 recent studies sampled black bears primarily in Yosemite Valley ($<$ 1% of total area in the park) and were not designed to determine if mother–offspring social learning is a mechanism responsible for black bears foraging on human foods. Understanding how black bears acquire the behavior to forage on human foods would benefit human–bear management programs because such information could help mitigate future bear incidents. For instance, black bears have caused thousands of incidents and millions of dollars in property damage in Yosemite (Hopkins and Kalinowski 2013). If mothers transmit the behavior to forage on human foods to their offspring primarily via social learning or genetic inheritance, then managers could concentrate their management programs on preventing females and their cubs from accessing developed areas.

The main goal of this study was to use genetic data and a new testing framework to determine if social learning from mothers to their offspring is at least partly responsible for free-ranging black bears foraging on human foods in Yosemite. This study tested 4 hypotheses. The first 3 hypotheses were provided by Mazur and Seher (2008): 1) the genetic inheritance hypothesis claims that bears inherit behavioral or temperamental dispositions that bias them toward foraging on particular foods in specific habitats; 2) the social learning hypothesis states that foraging behavior is transmitted via learning from mother to cub; and 3) the asocial learning hypothesis claims that foraging behavior is acquired via independent trial and error. A mechanism of transmission, as described in hypotheses 1 and 2, is difficult to discern when female bears and their independent offspring have similar foraging behavior. For this reason, I include a 4th, more general, hypothesis: the transmission hypothesis. This hypothesis states that bears transmit foraging behavior to their offspring via genetic inheritance, social learning, or both. We did not test a dispersal hypothesis, which states that independent bears are likely to have the same foraging behaviors as their relatives because they occupy similar habitats or areas as their relatives, thereby independently learning to forage. Evidence suggests that related and nonrelated bears use both developed and undeveloped areas in Yosemite, regardless of their sex, age class, or foraging behavior (e.g., many bears forage on natural foods exclusively in Yosemite Valley, the largest developed area in the park [Graber 1981; Matthews et al. 2006; Mazur 2008; Hopkins et al. 2012]).

I tested predictions deduced from the 4 hypotheses. I estimated relatedness coefficients and most probable relationships (parent–offspring, full-siblings, half-siblings, and unrelated) for each possible combination of 2 independent bears ($\geq$ 2 years old) sampled throughout Yosemite in 2004–2007. I also assigned each bear a foraging classification of "conditioned to forage on human foods" (FC) or "not conditioned to forage on human foods" (NFC) using previous classifications and isotopic methods from Hopkins et al. (2012); this strategy reduced bias associated with classifying bears and allowed me to sample bears throughout their lives and throughout the park.

My testing framework was based on the rationale that if the asocial learning and genetic inheritance hypotheses did not have statistical support, then social learning is primarily responsible for the transmission of black bear foraging behavior. For the 1st analysis, I used estimated relatedness coefficients (expressed as $\bar{r}$) to test predictions deduced from the asocial learning and transmission hypotheses. The asocial learning hypothesis predicts that female bears ($n = 72$) with the same foraging behavior (e.g., FC-FC used as an example below) are not more related than the sampled population (hereafter, all-bears) is related (equation 1), whereas the transmission hypothesis predicts that female bears with the same foraging behavior are more related than the sampled population is related (equation 2):

$$♀\,\bar{r}_{\mathrm{FC-FC}} = \bar{r}_{\mathrm{all-bears}} \tag{1}$$

and

$$♀\,\bar{r}_{\mathrm{FC-FC}} > \bar{r}_{\mathrm{all-bears}}. \tag{2}$$

I did not include male bears ($n = 78$) in this 1st analysis for 2 reasons. First, male bears do not rear cubs and therefore cannot transmit foraging behavior to their offspring via social learning. Second, relatedness analysis cannot discriminate between mother–son pairs and father–daughter pairs. Although male bears cannot pass foraging behavior to their offspring via social learning, they may be able to pass foraging behavior to their offspring via genes. If the transmission hypothesis was supported by the data, I then used male bears to generate additional predictions deduced from the social learning (equation 3) and the genetic inheritance (equation 4) hypotheses:

$$♂\,\bar{r}_{\mathrm{FC-FC}} = \bar{r}_{\mathrm{all-bears}} \tag{3}$$

and

$$♂\,\bar{r}_{\mathrm{FC-FC}} > \bar{r}_{\mathrm{all-bears}}. \tag{4}$$

If male bears with the same foraging behavior were no more related than the sampled population is related (equation 3), I failed to reject the social learning hypothesis. Alternatively, evidence supported the genetic inheritance hypothesis if male bears with the same foraging behavior were more related than the sampled population is related (equation 4).

For the 2nd analysis, I grouped relatives by behavioral classification and conducted a series of chi-square goodness-of-fit tests. If the foraging behavior of black bears is acquired via asocial learning, and I compare mother–daughter pairs by behavioral group (e.g., FC-FC used as an example below), then the number of observed pairs with the same foraging behavior will be similar to the number expected (equation 5). On the other hand, if foraging behavior is transmitted from mother to offspring, and I compare mother–offspring pairs by behavioral group, then more pairs of bears with the same foraging behavior will be observed (Obs) than expected (Exp; equation 6):

$$\mathrm{mother_{FC}daughter_{FC}}\text{: } \mathrm{Obs} = \mathrm{Exp} \tag{5}$$

and

$$\mathrm{mother_{FC}daughter_{FC}}\text{: } \mathrm{Obs} > \mathrm{Exp}. \tag{6}$$

If the asocial learning hypothesis was rejected (equation 5), and the transmission hypothesis had support (equation 6), I then used father–son pairs to generate additional predictions deduced from the social learning (equation 7) and the genetic inheritance (equation 8) hypotheses:

$$\mathrm{father_{FC}son_{FC}}\text{: } \mathrm{Obs} = \mathrm{Exp} \tag{7}$$

and

$$\mathrm{father_{FC}son_{FC}}\text{: } \mathrm{Obs} > \mathrm{Exp}. \tag{8}$$

The genetic inheritance hypothesis had support if more father–son pairs with the same foraging behavior were observed than expected (equation 8). Lastly, if no support is evident for genetic inheritance, I conducted an additional test on all parent–offspring pairs:

$$\mathrm{parent - offspring}\text{: } \mathrm{Obs} > \mathrm{Exp}. \tag{9}$$

If fathers and sons do not have similar foraging behavior, then the same is likely true for fathers and daughters. If more parent–offspring pairs with the same foraging behavior are observed than expected, and these observed bears are in greater number than those observed in test 6, then I assume most of the additional pairs are mothers and sons; the only parent–offspring combination not accounted for. This latter case would provide additional evidence for social learning because both mother–offspring pairs are accounted for in the analysis.

MATERIALS AND METHODS

Study area.—Yosemite National Park encompasses approximately 3,080 km^2 on the west slope of the Sierra Nevada in central California. Elevations range from 648 m in the foothills on the western boundary to 3,997 m along the Sierra Crest. The climate in Yosemite is characterized as Mediterranean with warm, dry summers and cool, moist winters. The backcountry of Yosemite includes 2,770 km^2 of roadless wilderness.

Yosemite attracts 4 million visitors each year. Most people visit Yosemite Valley (18 km^2; 1,200 m elevation) in April–October, the same months when bears are active. Since the early 1900s, Yosemite Valley has been recognized as an area to view black bears foraging on both human foods and natural foods. Bears that forage on natural foods exclusively eat these foods in the spring at lower elevations, such as Yosemite Valley, and follow snowmelt and sprouting vegetation upslope in the summer (Graber 1981; Graber and White 1983). In the fall, bears return to these lower elevations for acorns and berries (Graber 1981; Graber and White 1983). During the early 1900s black bears were rarely seen above 2,500 m (Grinnell and Storer 1924), but are now commonly sighted at higher elevations. Studies conducted in the 1970s suggested that bears increased occupation of these higher elevations to seek human foods (Graber 1981; Keay and van Wagtendonk 1983).

Sampling.—Unlike Mazur and Seher (2008) and Breck et al. (2008), I sampled bears park-wide for this study ($n = 150$ [Supporting Information S1, DOI: 10.1644/13-MAMM-A-009.S1]). This sampling strategy was especially important because wildlife management personnel commonly transport young bears, regardless of their foraging behavior, from Yosemite Valley (or other developed areas) to other locations in the park (Hopkins and Kalinowski 2013). Wildlife management personnel captured bears and collected hair in accordance with guidelines approved by the American Society of Mammalogists (Sikes et al. 2011). Wildlife management personnel classified bears as FC if they were observed foraging on human foods in Yosemite. In general, bears outside Yosemite Valley (approximately 99% of the park) are rarely marked and monitored (Greenleaf 2005). As a result, the foraging behaviors of many bears in the park are typically unknown to management staff. I used behavioral classifications and methods developed in Hopkins et al. (2012) to reduce error associated with classifying bears (especially bears classified as NFC via radiotelemetry). Hopkins et al. (2012) used nitrogen isotope (δ^{15}N) data derived from the hair of known bears classified as FC and as NFC to build a logistic regression model used to predict the foraging behavior of bears sampled throughout the park. They reported that 32 bears (1 bear of 33 in their study was not successfully genotyped) foraged on human foods and 111 bears foraged on natural foods exclusively (Hopkins et al. 2012). In this study, I used these bears and included genetic and behavioral data for 7 bears not included in the study of Hopkins et al. (2012). Wildlife management personnel classified 4 of these 7 bears as FC, and I predicted the foraging behavior of 3 bears (1 as FC and 2 as NFC) using the model provided in Hopkins et al. (2012; Supporting Information S1). I conducted the following statistical analyses on 37 FC bears and 113 NFC bears.

Analytical procedures.—I used genotypes from 8 microsatellite loci provided by Hopkins et al. (2012) and from 2 additional loci (G10L and MU59—Paetkau and Strobeck 1994; Taberlet et al. 1997; Supporting Information S2, DOI: 10.1644/13-MAMM-A-009.S2) to estimate coefficients of relatedness and most probable relationship. I used the maximum-likelihood estimator of Milligan (2003 [using ML-RELATE—Kalinowski et al. 2006]) to estimate coefficients of relatedness and most probable relationship for all combinations of 2 bears in the data set. I note that 5 of 5 cubs, not used in this study because they are not independent bears, were linked successfully to their known mothers using ML-RELATE (Supporting Information S1). I then categorized all pairs of bears into 3 behavioral groups. I defined pairs of bears that both forage on human foods as FC-FC; pairs of bears that both foraged on natural foods as NFC-NFC; and pairs of bears that have different foraging behaviors as FC-NFC (which denotes both FC-NFC and NFC-FC pairs).

I used bootstrap resampling to test predictions for the 1st analysis because the $\bar{r}$ distributions are nonnormal and each behavioral group was a subset of the all-bear distribution. For example, to test $♀\bar{r}_{\text{FC-FC}} = \bar{r}_{\text{all-bears}}$, I randomly selected 14 bears (i.e., the number of female FC bears) from the all-bear data set 10,000 times. I then calculated $\bar{r}$ for each 14-bear matrix; each $\bar{r}$-value was used to generate the bootstrap distribution of the sample mean. I noted the number of times each bootstrap $\bar{r}$ estimate was greater than or equal to $\bar{r}$ for the observed data. This fraction is the P-value for the null hypotheses. For the 2nd analysis, I grouped all mother–daughter, father–son, and parent–offspring dyads by behavioral classification and conducted a series of chi-square goodness-of-fit tests.

Mazur and Seher (2008) showed that some bears switch their foraging behavior during certain years (Fig. 1B). For instance, they found that 17% of adult females ($n = 32$) that foraged on human foods as independents foraged on natural foods exclusively when rearing their cubs. Because I expected that some behavioral groups were misclassified as FC-NFC because of females switching foraging behavior, and that some bears likely learned to forage on human food independently as innovators (Reader 2003), I used an $\alpha = 0.10$ to test predictions for both analyses (Cohen 1988). I conducted all statistical tests using R (2.13.0—R Core Team 2012).

RESULTS

I report 4 results from the $\bar{r}$ analysis. First, female FC-FC pairs had the largest $\bar{r}$ of all behavioral groups, which was significantly larger than $\bar{r}$ for the sampled population (Table 1); this result supports the transmission hypothesis. Second, male FC-FC pairs had the smallest $\bar{r}$ of all behavioral groups, which was smaller than $\bar{r}$ for the sampled population (Table 1); this result fails to reject the social learning hypothesis (given that the transmission hypothesis had support) and does not support the genetic inheritance hypothesis. Third, female FC-NFC pairs were also more related than the sampled bear population is related, but male FC-NFC bears were not (Table 1); as expected, some behavioral groups were likely misclassified as FC-NFC because of females switching foraging behavior and some bears in the sampled population are likely innovators.

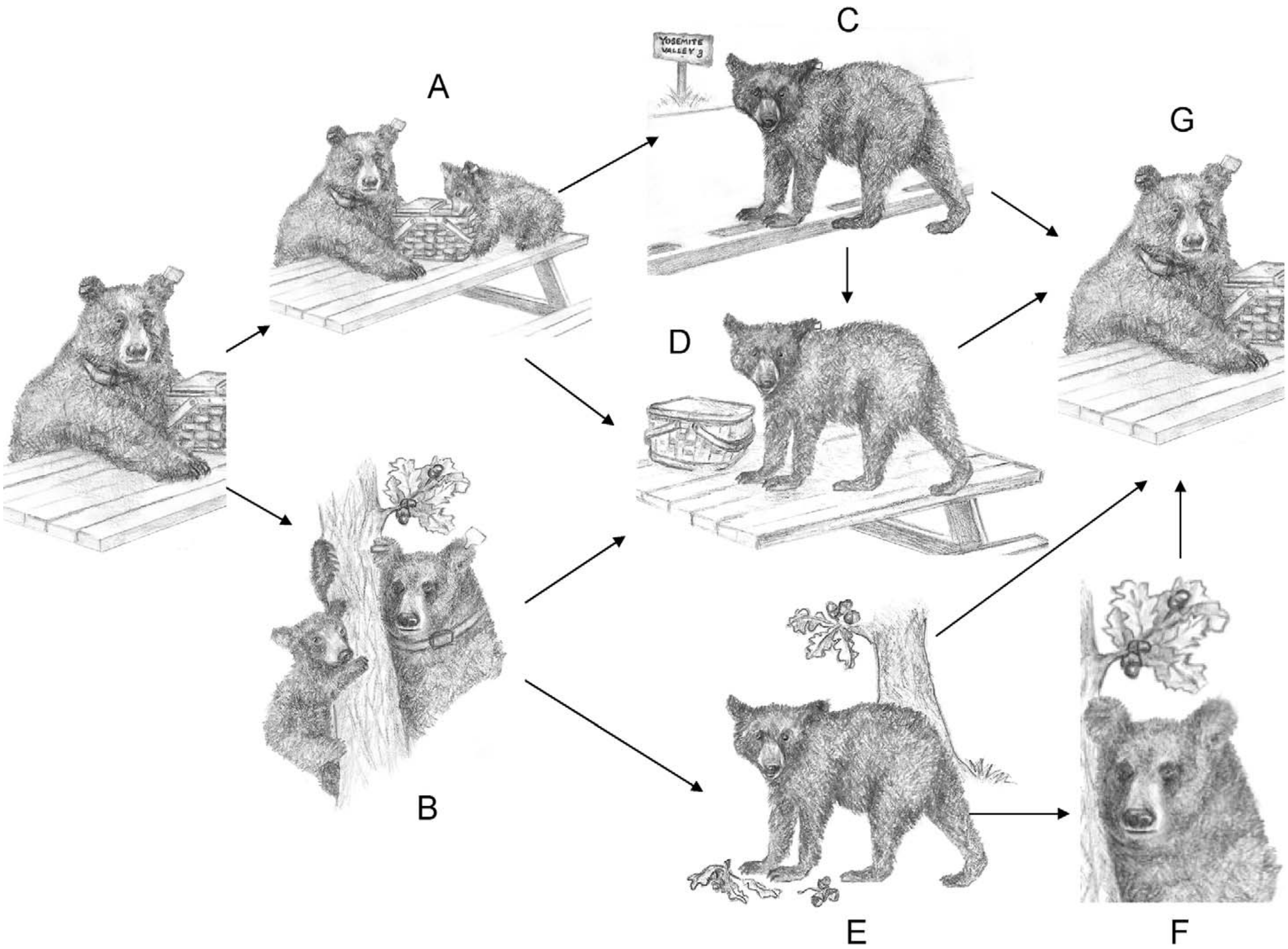

Fig. 1.—Potential pathways to foraging on human foods as an independent bear (*Ursus americanus*) in Yosemite National Park when reared on human foods or on natural foods exclusively. A) A female bear that forages on human foods as an independent usually rears her cubs on human foods in developed areas; however, B) some of these adult bears rear their cubs on natural foods exclusively in undeveloped areas. C) Following independence, management personnel often transport yearling bears that forage on human foods to undeveloped areas. Transported yearlings either C) establish a new home range outside their natal areas or D) return to developed areas to seek out human foods. D) Yearlings that were reared as cubs in developed areas (and not captured and transported) disperse to other areas where they can forage on human foods. B) The cub that forages on natural foods exclusively either D) learns to forage on human foods independently as a yearling or E) continues to forage on natural foods exclusively as a yearling, and F) eventually, as an adult. G) Regardless of rearing method, adult bears can learn to forage on human foods during some stage of development, either socially or asocially.

Fourth, both female and male NFC-NFC bears were not more related than the sampled population was related (Table 1), which does not support the transmission hypothesis.

I report 4 sets of results from the relationships analysis. First, mother–daughter pairs were sorted into behavioral groups in a significantly different manner than expected, but father–son pairs were not (Table 2). More FC-FC mother–daughter pairs were observed than expected, which supports the transmission hypothesis; this was not the case for father–son relationships (Table 2). This combination of results offers more support for the social learning hypothesis than the genetic inheritance hypothesis. Second, parent–offspring pairs also were sorted into behavioral groups in a significantly different manner than expected (Table 2). More FC-FC parent–offspring pairs were observed than expected, providing additional support for the social learning hypothesis. Third, more FC-NFC mother–daughter pairs and parent–offspring pairs were observed than expected (Table 2); as expected, some behavioral groups were likely misclassified and some bears in the sampled population are likely innovators. Fourth, fewer NFC-NFC pairs were observed than expected for all relationships (Table 2), which does not support the transmission hypothesis.

Discussion

Results from both analyses suggest that mother–offspring social learning is the primary mechanism responsible for black

Table 1.—Mean *r*-value ($\bar{r}$) of behavioral groups by category for black bears (*Ursus americanus*) sampled in Yosemite National Park, California, 2004–2007. *n* denotes the number of related pairs in each group. 95% *CI* = 95% confidence interval; FC = conditioned to forage on human foods; NFC = not conditioned to forage on human foods.

Behavioral groups	*n*	$\bar{r}$	95% *CI*	*P*-value
Sampled population	11,175	0.090		
FC-FC	666	0.098	0.090, 0.106	0.147
FC-NFC	4,181	0.091	0.087, 0.095	0.433
NFC-NFC	6,328	0.089	0.087, 0.092	0.708
Female bears				
FC-FC female	91	0.117	0.093, 0.141	0.067
FC-NFC female	812	0.101	0.091, 0.111	0.065
NFC-NFC female	1,653	0.093	0.088, 0.098	0.277
Male bears				
FC-FC male	253	0.075	0.065, 0.086	0.937
FC-NFC male	1,265	0.085	0.078, 0.092	0.853
NFC-NFC male	1,485	0.085	0.078, 0.092	0.850

bears foraging on human foods in Yosemite. Many bears that forage on human foods likely learned this behavior from their mother during the first 16–18 months of life. Following independence, these bears continued to seek out human foods, although this behavior is not always consistent. As expected, evidence from both analyses suggests that some bears acquired the behavior to forage on human foods as independents. Innovators likely help sustain the trait in the population (Lefebvre and Giraldeau 1996; Reader 2003) because many bears that forage on human foods are eventually killed (Hopkins and Kalinowski 2013).

Evidence from the relatedness analysis suggests that mother–offspring social learning is the primary mechanism responsible for black bears foraging on human foods in Yosemite. Breck et al. (2008) also conducted relatedness analyses (using both parametric and nonparametric tests) and provided an alternate conclusion. In contrast to this study, they concluded that black bears do not acquire the behavior to forage on human foods strictly from social learning or genetic inheritance because foraging behavior does not partition along genetically related lineages. They used their entire sample (males and females) to test for differences in $\bar{r}$ among behavioral groups (H$_0$: $\bar{r}_{\text{FC-FC}} = \bar{r}_{\text{NFC-NFC}} = \bar{r}_{\text{FC-NFC}}$). They deduced the following prediction for the transmission hypothesis: $\bar{r}_{\text{FC-FC}} > \bar{r}_{\text{FC-NFC}}$ and $\bar{r}_{\text{NFC-NFC}} > \bar{r}_{\text{FC-NFC}}$. They found that FC-FC pairs in both study areas had significantly greater $\bar{r}$ (especially in Yosemite) than FC-NFC pairs, but they did not find the same pattern for NFC-NFC bears (Breck et al. 2008). Instead, they found that FC-NFC pairs had higher $\bar{r}$ than NFC-NFC pairs. Their $\bar{r}$ analysis was more appropriate for testing genetic inheritance, which generates a prediction that related bears are either FC-FC or NFC-NFC; however, this prediction is invalid based on what was learned from Mazur and Seher (2008). Unlike Mazur and Seher (2008), Breck et al. (2008) did not observe females switch from foraging on human foods as independents to rearing their cubs in undeveloped areas on natural foods exclusively (S. Breck, USDA National Wildlife Research Center, pers. comm.). If they had, they would have expected some FC-NFC pairs. In addition, FC-NFC pairs should have been expected, because father–offspring pairs were included in their analysis. Because males do not participate in rearing cubs, FC-NFC pairings between father and offspring are likely to occur in the sample unless genetic inheritance controls foraging behavior.

Table 2.—Observed and expected behavioral groups by relationship for black bears (*Ursus americanus*) sampled in Yosemite National Park, California, 2004–2007. Relationships were estimated using ML-RELATE (Kalinowski et al. 2006). FC = conditioned to forage on human foods; NFC = not conditioned to forage on human foods.

Relationships	Observed	Expected	χ^2	*P*-value
Mother–daughter			16.2	0.031
FC-FC	8	5		
FC-NFC	50	40		
NFC-NFC	69	82		
Father–son			6.9	0.463
FC-FC	6	6		
FC-NFC	36	31		
NFC-NFC	32	37		
Parent–offspring			1.5	< 0.001
FC-FC	38	24		
FC-NFC	169	148		
NFC-NFC	191	226		

Evidence from the relationship analysis is consistent with results from the relatedness analysis, suggesting that mother–offspring social learning is the primary mechanism responsible for black bears foraging on human foods in Yosemite (Table 2). I assume that because the number of observed father–son pairs was equal to the number of expected pairs, the same is likely true for father–daughter pairs. As a result, most of the excess parent–offspring pairs that were observed are likely mother–son pairs; however, the actual number of father–daughter versus mother–son pairs cannot be discerned from the male–female pairings.

A relatively large number of FC-NFC mother–daughter and parent–offspring pairs and a significantly large $\bar{r}$ for female FC-NFC bears suggest that some bears learned to forage on human foods as innovators (Tables 1 and 2). Furthermore, some behavioral groups were likely misclassified as FC-NFC. For instance, female bears that forage on human foods as independents but switch their foraging behavior when rearing cubs (Fig. 1B) could have been sampled during a year when they were independent (Fig. 1E). Lastly, the behavior of innovators and misclassifications as described likely contributed to fewer NFC-NFC pairs observed than expected for all relationships (Table 2).

Misclassifying yearling bears that forage in undeveloped areas on natural foods exclusively (or "wild bears") would bias the results of Mazur and Seher (2008). In Yosemite, yearlings that forage on human foods are commonly transported from Yosemite Valley to undeveloped areas in the park (Hopkins and Kalinowski 2013; Fig. 1C). For instance, in 1995–2006 (when bears were captured in the study by Mazur and Seher [2008]) Yosemite personnel captured and transported a minimum of 25 yearlings (16 from Yosemite Valley) from developed areas to undeveloped areas (Yosemite National Park, unpublished data). Mazur and Seher (2008) tagged some yearling bears but did not use radiotelemetry to monitor these individuals. Fifty-three yearlings were classified as wild "largely by default" because they were not observed in developed areas (Mazur and Seher 2008:1504). If yearlings were not monitored following their transport using radiotelemetry, then the assumption that they forage on natural foods exclusively is not valid. This is especially the case for yearlings in Yosemite, because bears are not regularly monitored outside Yosemite Valley (Hopkins and Kalinowski 2013). Instead, the foraging behaviors of these bears were unknown by the end of their 2nd year. As a result, the conclusion that "cubs reared in the wild tended to forage in the wild as independents" is not necessarily an accurate one (Mazur and Seher 2008:1506).

Evidence from both this study and that of Mazur and Seher (2008) suggests that mothers transmit the behavior to forage on human foods to their offspring. Mazur and Seher (2008) showed that the rearing method (of mothers that forage on human food only) had a significant effect on whether cubs would forage on human foods as yearlings. Mazur and Seher (2008) also showed compelling evidence of mother–offspring social learning by monitoring 2 female bears that switched their rearing behavior. These females reared their 1st litter of cubs on natural foods and subsequent litters on human foods. Yearlings from the 1st litter were later classified as NFC and yearlings from subsequent litters were classified as FC. Unlike Mazur and Seher (2008), I used a new framework to test both the social learning and the genetic inheritance hypotheses, independently. I sampled independent bears park-wide and compared the foraging behavior of related bears. Even though some mothers that forage on human food as independents occasionally switch their foraging behavior when rearing cubs, potentially confounding the results in this study (due to an excess of FC-NFC pairs), I found highly suggestive evidence that these mothers often transmit the behavior to forage on human foods to their offspring via social learning. I also found indirect evidence suggesting that some bears behave as innovators and seek out human foods asocially. Although neophilia or boldness to explore developed areas may result from polygenic inheritance, neither Breck et al. (2008) nor this study found evidence suggesting that foraging behavior is acquired primarily via genetic inheritance.

No studies discussed here have provided strong evidence suggesting that the behavior of foraging on natural foods exclusively is transmitted from mother to offspring or maintained through time. Although a high number of NFC-NFC pairs were observed in my sample (Table 2), results from this study do not lend statistically significant support to the claim that black bears learn to forage on natural foods from their mothers. Innovators, misclassifications, and a high number NFC bears in the sample likely diluted any statistical signal suggesting social learning in NFC bears. I assume, however, based on results for FC-FC bears, that offspring likely learn to forage on natural foods from their mothers and that some of these offspring also learn to forage on human foods; the latter determined by whether or not mothers rear their offspring in developed areas on human foods.

Future studies that investigate the foraging behavior of free-ranging mammals with prolonged mother–offspring relationships should include both a longitudinal and genetic component. I recommend tracking known mothers and their offspring continuously throughout their entire lives. Although these studies are costly and time intensive (Lonsdorf and Bonnie 2010), wildlife managers could collect data on foraging behavior during their long-term demographic studies. Researchers also should identify females that switch foraging behavior when they rear their offspring. Tracking these individuals and their offspring through time could provide compelling evidence for social learning. It is also important to determine what forms of social learning occur in parent–offspring pairs: local enhancement (Thorpe 1963; Sherry and Galef 1984; Galef and Giraldeau 2001; Whiten and Ham 2002), imitation (Whiten and Ham 2002; Moore 1996), teaching (Thornton and Raihani 2010), or tutoring (Caro and Hauser 1992; Caro 1994; Kitchener 1999). Last, it is important to investigate asocial learning in cubs and to identify the genetic or environmental factors responsible for independent animals having neophobic or neophilic tendencies to forage in familiar or novel environments, respectively. Collectively, these research efforts are essential to understanding the foraging behavior of free-ranging mammals with prolonged mother–offspring relationships and to directing human–wildlife management efforts.

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SUPPORTING INFORMATION

SUPPORTING INFORMATION S1.—Isotope values, genotypes, and behavioral classifications for black bears sampled in Yosemite National Park, USA, 2004–2007.

Found at DOI: 10.1644/13-MAMM-A-009.S1

SUPPORTING INFORMATION S2.—Comparison of allelic data for black bears sampled in Yosemite National Park in 2001–2002 and 2004–2007.

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