



Socially learned foraging behaviour in wild black bears, *Ursus americanus*

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To date, research on social learning has been limited mainly to only a few taxa in captive or seminatural settings. We undertook a quantitative study of social learning in free-ranging black bears at Sequoia and Yosemite National Parks, U.S.A. from 1995 to 2006. We tested the hypothesis that food-conditioned foraging behaviour (foraging on human food in developed areas) by some bears is transmitted vertically from sows to cubs. Food conditioning in young bears was strongly related to their rearing conditions. Nine wild sows reared 20 cubs in the wild, with 18 (90%) of the cubs remaining wild by the end of their second year. By contrast, of 79 cubs reared by food-conditioned mothers, 31 were reared in the wild and 48 were reared on anthropogenic food sources. Eighty-four per cent (26/31) of those reared in the wild foraged in the wild as independents, and 81% (39/48) of those reared on anthropogenic food continued to exploit this resource later in life. The outcome of the cubs was determined more by where the cubs were reared than by whether the sow was food conditioned.

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Social learning occurs when an animal acquires a new behaviour as a result of observing or interacting with another animal (Heyes 1994; Galef & Laland 2005). Although a great deal of research on social learning has occurred in some mammalian taxa (e.g. primates and rodents), there has been little research on most species (Lefebvre & Giraldeau 1996; Perry 2003). Furthermore, most research to date has been conducted in laboratories (Perry 2003) or outdoor pens (Griffin & Evans 2003; Page & Ryan 2006). The lack of systematic data on wild animals is due largely to the difficulties of observing animals in the wild and the inability to control their experiences (Whitehead 2003; Krützen et al. 2005); hence most observations are anecdotal (Terkel 1996; Boran & Heimlich 1999;

Kitchener 1999; Nel 1999; Perry 2003; Whitehead 2003; Krützen et al. 2005).

To quantify social learning, one must observe (1) the presence or absence of a learning experience (transmission variable) for each individual animal, and (2) whether the behavioural outcome was different for those animals that did versus those that did not have a learning experience (outcome variable) (West et al. 2003). Heterogeneity of learning experiences and outcomes within the studied group are critical for reaching any conclusions (Perry 2003).

Learning ability has been correlated with large brain size, well-developed memory, behavioural plasticity and curiosity (Lefebvre & Giraldeau 1996; Fragaszy & Visalberghi 1996; Reader 2003). Bears have all of these traits (Gittleman 1986; Gilbert 1999). The most likely context for social learning in black bears is during the prolonged mother–cub association (Gilbert 1999) because even minimal parental care has been hypothesized to select for social learning (Göth & Evans 2005). During this period, it is likely that cubs learn about predators, dietary choices and foraging sites (Gilbert 1999).

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We studied social learning in free-ranging black bears at Sequoia and Yosemite National Parks, U.S.A., testing the hypothesis that the use of developed areas as foraging sites was transmitted vertically from sows to cubs. For the purposes of this paper, foraging on human food or trash in developed sites is defined as 'food-conditioned' foraging behaviour. Alternately, foraging on natural (nonanthropogenic) food is 'wild' foraging behaviour.

Food-conditioned foraging by black bears, once encouraged as entertainment in National Parks (Graber & White 1983), is now unacceptable; it results in human injuries, property damage and ultimately dead bears (Matthews et al. 2006). Although identifying the source of food-conditioned foraging behaviour will elucidate how animals acquire behaviours in the wild, it also has the potential for assisting wildlife managers in their efforts to eliminate its occurrence.

Here, we introduce competing hypotheses for how food-conditioned foraging behaviour is spreading in black bears.

(1) Bears inherit behavioural or temperamental predispositions to forage in certain areas. This hypothesis is based on the theoretical expectation that animals inherit behavioural tendencies such as neophobia and neophilia that predispose them to respond in particular ways to environmental challenges (Biossy 1995; Dingemanse et al. 2002; Reale et al. 2007). Neophobic tendencies may bias bears towards foraging in the familiar wild environment, whereas neophilic tendencies would bias them to venture into potentially hazardous human environments. The implication is that a cub's foraging behaviour, when it becomes independent, is predictable from the behaviour of its mother.

(2) Food-conditioned foraging behaviour is acquired through individual learning. Here we assume that social learning is unimportant and that individuals learn exclusively through their own exploration and trial and error (Thorpe 1963; Heyes 1994). This implies that the likelihood of a cub becoming food conditioned is largely independent of its mother's behaviour or mode of mothering.

(3) Food-conditioned foraging behaviour is transmitted vertically, through social learning, from sows to cubs. There are various mechanisms for social learning including imitation, local enhancement and even direct tutoring (Galef 1977; Sherry & Galef 1984; Caro & Hauser 1992; Whiten & Ham 2002). We are not able to tease apart all of these possibilities. However, their essential commonality is that one individual learns some aspect of its foraging behaviour from another (Heyes 1994; Whiten & Ham 2002). The implication is that a cub's behaviour, once it is independent, is predictable from the sow's mode of rearing, whether in the wild or in human environments.

METHODS

Study Area

Sequoia and Yosemite National Parks together cover 4725 km² on the western slope of the Sierra Nevada mountains in California. They range in elevation from

418 m in the low western foothills to 4417 m on the crest of the Sierra and are composed largely of rugged mountainous terrain. Vegetation types include chaparral, oak woodland and savannah, upland hardwood forest, conifer forest, woodland, meadows and alpine plant communities. The region's Mediterranean climate is characterized by wet snowy winters and long dry summers (Stephenson 1988). Approximately four million visitors come to the two parks each year (National Park Service 2006). In Sequoia, there are seven campgrounds with 560 campsites and five developed picnic areas. In Yosemite, developed areas include 13 campgrounds with almost 2000 campsites and five developed picnic areas.

General Methods

In both Sequoia and Yosemite National Parks, food-conditioned sows are regularly trapped and marked with coloured and uniquely numbered eartags (Allflex International, Dallas, Texas, U.S.A.; Dalton Supplies, U. K.) to distinguish individuals. In Sequoia but not Yosemite, wild sows whose home ranges overlapped with developed areas were also trapped and marked during this study for an unrelated research project. We then trapped and marked all cubs of marked sows so we could monitor their behaviour when they became independent.

From 1995 to 2006 in Yosemite and from 2000 to 2006 in Sequoia, cubs that lacked natural distinguishing marks were caught using a combination of culvert traps, Havahart traps and nets. In Sequoia, cubs were immobilized with 4.4 mg/kg of Telazol, whereas in Yosemite, cubs were immobilized with 4.3 mg/kg of ketamine and 2.1 mg/kg of xylazine per park policy. In both areas, cubs were marked with metal or plastic eartags (Hasco Tag Co., Dayton, Kentucky, U.S.A.; Dalton Supplies) and standard measurements were taken. All handling operations were approved by the National Park Service and the U.C. Davis Animal Care and Use Committee (IACUC no. 11520).

We characterized the foraging behaviour, location and activity for each sow and cub in developed areas based on our daily observations. We, our field crews or other trained rangers were nearly continuously present to record bear activity in all developed areas between 0700 and 0200 hours. Characterization of bears in wild areas was largely by default and verified by daily efforts to locate each bear. It is unlikely that we missed many instances of sows with cubs entering developed areas because cubs are popular with the public and sightings are usually reported to our offices multiple times. Although bears did enter developed areas when no staff was working (e.g. visitor reports of bears late at night), they were usually the same bears that were present earlier in the night. Generally, these events led to staff shifting hours for the next week to verify the identity of the bears.

There were five variables of interest in this study: park, sow identity, sow behaviour, rearing method and cub outcome. The park was Sequoia or Yosemite. Sow identity was the identity of individual sows, which may have reared more than one cub in more than one litter. Preliminary observations of the three behavioural variables revealed that there was not enough variability for

continuous measures; most bears either never entered developed areas or entered them regularly. All bears foraged in wild areas for at least some part of each day. Therefore, all variables were defined as dichotomous.

Sow behaviour was used to distinguish between food-conditioned sows and wild sows. A food-conditioned sow was defined as a sow that was seen foraging on human food or trash within developed areas at least three times. A sow that did not show these behaviours was classified as wild.

Rearing method was the transmission variable. It defined the type of foraging areas that cubs encountered during their first year. If sows brought their cubs into developed areas at least three times while the sows foraged on human food, rearing method was classified as developed. If sows reared cubs away from developed areas or left cubs in trees outside of developed areas while the sow foraged inside, rearing method was classified as wild.

The final variable, cub outcome, described whether a cub foraged in developed or wild areas between the time it was independent from its mother and the end of its second year. Bears are most likely to forage in new areas at that time (Lee & Vaughan 2003). If a cub foraged in developed areas at least three times as an independent or was killed owing to its association with a developed area by the end of its second year, cub outcome was classified as food conditioned. If a cub was observed foraging only in wild areas after it was independent, cub outcome was classified as wild.

Data were analysed using a generalized linear mixed model to allow sow identity to be included as a random effect term. The park (Sequoia versus Yosemite), sow behaviour (food conditioned versus wild) and rearing method (developed versus wild) were included as fixed effects. We used cub rather than litter as the unit of analysis because cubs within the same litter often had different outcomes. All analyses were completed using SAS statistical software (version 9.1; Cary, North Carolina, U.S.A.). Statistical comparisons were considered significant at $\alpha = 0.05$.

RESULTS

Thirty-two sows with 99 cubs were included in this study; nine sows were classified as wild and 23 sows were classified as food conditioned (Table 1). Wild sows produced 20 cubs, with 18 (90%) of the cubs foraging exclusively in wild areas as independents. Food-conditioned sows produced 79 cubs, with 35 (44%) of the cubs, regardless of where they were reared, foraging exclusively in wild areas as independents. There was no significant difference between the average litter size of wild sows (mean = 1.7) and that of food-conditioned sows (mean = 1.8) ($F_{2,56} = 0.37$, $P = 0.693$). There were no obvious differences (e.g. gender, nutrition) between the cubs that remained wild and those that became food conditioned.

Foraging behaviours of independent cubs was strongly related to where they were reared. The wild sows reared all 20 of their cubs (100%) in wild areas. The food-conditioned sows reared 31 cubs (39%) in wild areas and the

Table 1. Effects of a sow's behaviour and rearing style on cubs' behaviour (measured as yearlings) in Sequoia and Yosemite National Parks, California

Sow behaviour	Rearing style	Cub behaviour
Food conditioned (F-C) (N=23)	Reared wild (N=31, 39%)	Food conditioned (N=5, 16%) Wild (N=26, 84%)
	Reared F-C (N=48, 61%)	Food conditioned (N=39, 81%) Wild (N=9, 19%)
Wild (N=9)	Reared wild (N=20, 100%)	Food conditioned (N=2, 10%) Wild (N=18, 90%)
	Reared F-C (N=0)	Food conditioned (N=0) Wild (N=0)

other 48 cubs (61%) in developed areas. Grouping the cubs strictly by how they were reared and not by their mother's behaviour, 44 (86%) of the 51 cubs that were reared in wild areas remained wild as independents, and only nine (19%) of the 48 cubs that were reared in developed areas remained wild as independents.

Using a generalized linear mixed model, we found that, after accounting for sow behaviour and park, rearing method had a highly significant effect on the cub outcome ($F_{1,66} = 15.23$, $P < 0.001$). The odds of a sow rearing a cub that became food conditioned by the end of its second year were 45 times higher if she reared the cub in developed versus wild areas (95% confidence interval = 6.4, 333.3). The effect of rearing condition remained significant ($F_{1,66} = 18.29$, $P < 0.001$) when the sow behaviour variable was omitted from the model, suggesting that, once cubs were independent, their foraging behaviour was determined by where they were reared and not by their mothers' behavioural type.

It is illuminating to look at the sows with multiple litters to determine whether they were consistent in rearing their cubs in wild or developed areas. Eighteen of the 32 sows had more than one litter during this study (Table 2). Of these, seven sows (three wild and four food conditioned) consistently reared their cubs in wild areas. Seven other sows (all food conditioned) consistently reared their cubs in developed areas. The four remaining sows (all food conditioned) reared one or more litters wild and then reared a litter in a developed area. There were no sows that first reared litters in developed areas and then switched to rearing later litters in wild areas. In two of the four instances where sows switched from rearing cubs in wild areas to rearing them in developed areas, the outcome for cubs also switched from wild to food conditioned. In the other two instances, one sow produced all wild yearlings. Results for the fourth sow's yearlings are unknown.

Of the 46 cubs that were food conditioned as independents, 22 died before the end of their second year. Sixteen of these deaths are attributable to their association with developed areas: eight were hit by cars, one was killed inside a garbage truck, one was stoned by visitors, one drowned in a sewage pond and five were killed by park management for public safety. In an attempt to save the

Table 2. Patterns of successive locations where black bear sows reared their cubs as a function of the sows' behaviour in Sequoia and Yosemite National Parks, California

Sow behaviour	Number of litters	Rearing location
Food conditioned (N=23)	≥2 (N=15)	4 of 15 sows reared cubs in wild areas 7 of 15 sows reared cubs in developed areas
	1 (N=8)	4 of 15 sows reared cubs in wild areas and then switched to reared cubs in developed areas 8 of 8 sows reared cubs in developed areas
Wild (N=9)	≥2 (N=3)	3 of 3 sows reared cubs in wild areas
	1 (N=6)	6 of 6 sows reared cubs in wild areas

other 30 bears, managers applied aversive-conditioning treatments to three bears, with unknown results, and experimentally relocated the remaining 27 to undeveloped outlying areas. Unlike relocation of adults (which is known to fail; National Park Service 1989), relocation of cubs and yearlings may succeed if these bears disperse into undeveloped areas. Six of the 27 relocated bears were killed (one by park management and five by other parties), six bears were known successes (although one was later hunted legally), one bear died for unknown reasons, and the fate of 14 others is unknown.

DISCUSSION

The strong effect of the transmission variable, rearing method, on the behavioural outcome of cubs as independents is consistent with the hypothesis that bears become food conditioned through social learning. Cubs that were reared in developed areas tended to forage in developed areas when they became independent, whereas cubs reared in the wild tended to forage in the wild as independents. Whereas cubs learned about developed areas from their mothers, they may have learned to eat the food on their own, perhaps through trial and error, making the mechanism of transmission local enhancement (Galef & Giraldeau 2001; Whiten & Ham 2002). Another mechanism that may be occurring in some situations is imitation, a process by which one individual learns something intrinsic about an action from another individual (Moore 1996; Whiten & Ham 2002). Anecdotal evidence from our study includes observations of independents breaking into vehicles in the same manner as their mother (R. Mazur, unpublished data).

A less parsimonious explanation is that sows are actively tutoring their cubs to forage in developed areas. Tutoring requires a teacher to modify its behaviour, at some cost, for the benefit of a naïve pupil, which then acquires the

behaviour faster than it otherwise would (Caro & Hauser 1992). Tutoring has been noted in several felids, particularly cheetahs (Caro 1994), and has been suggested in other species (Kitchener 1999). We have observed sows pushing cubs into buildings and vehicles to retrieve food rewards (R. Mazur, unpublished data).

In our study, the way a cub was reared, rather than the behaviour of its mother, was the main predictor of the cub's behaviour as an independent. This rules out heritable temperamental predispositions as the primary means by which food-conditioned foraging behaviour arises. However, 19% of cubs reared in developed areas did forage exclusively in the wild once independent, and 14% of cubs reared in wild areas foraged in developed areas as independents. It is possible that these exceptions were guided by inherited instincts such as neophobia or neophilia (Biossy 1995; Reale et al. 2007), a possibility we could not fully test.

Because the likelihood of a cub becoming food conditioned was not independent of its mother's behaviour or mode of rearing, we could also rule out individual learning as the primary means by which food-conditioned foraging behaviour arises. With local enhancement, individual learning occurred, but only after opportunities were presented due to social learning (Sherry & Galef 1984). However, some individual learning did occur in the absence of social learning, both within the group of cubs that were reared by wild sows in wild areas and within the group that were reared by food-conditioned bears in wild areas. Cubs that learn individually act as innovators (Lefebvre & Giraldeau 1996; Reader 2003). They establish new behaviours, such as food-conditioned foraging, in a population. If all individuals showing a given behavioural trait are removed from a population, innovators may reestablish the trait.

Our conclusion that social learning is the dominant mode of transmission for food-conditioned foraging behaviour is strengthened further when one considers the four sows that switched rearing methods with different litters. In at least two of these cases, sows reared their first litters in the wild and the cubs remained wild. These same two sows reared subsequent litters in developed areas and these cubs became food conditioned. Most sows (83%) did not switch their rearing style, allowing managers to predict how future cubs would be reared and to plan ahead for potential future problem bears. In such cases, they might close the foraging area to the public, have technicians haze the bear out of the area or consider destruction of the sow.

There are questions in the literature as to whether socially learned behaviours form traditions in the wild and whether there are clusters of these behaviours that may be defined as cultures. Since there are so few species for which social learning has been addressed in the wild, there is little evidence available with which to consider these questions (Perry 2003). Furthermore, definitions of tradition and culture vary, leading to varied conclusions (Fragaszy & Perry 2003). For the purposes of addressing these questions, we define tradition as the continuance of a behavioural trait that is acquired by an innovator by repeated social transmission across or within generations

(Fragaszy & Perry 2003). For culture, we use a more restrictive definition; that is, the trait must spread to the point of becoming a population-level characteristic (Whiten et al. 1999).

Once initiated by an innovator, food-conditioned foraging behaviour in black bears does persist across multiple generations (National Park Service 2001), potentially putting it in the realm of traditions, but does it constitute culture? Although food-conditioned foraging behaviour is at times a population-level characteristic (Meagher & Fowler 1989), we have yet to quantify consistent variation in strategies used by different clusters of individuals. Until that is possible, as was done with wild chimpanzees, *Pan troglodytes* (Whiten et al. 1999), we hesitate to classify nuisance foraging behaviour as a culture.

Finally, we ask whether social learning of food-conditioned foraging is adaptive or whether it leads bears into an ecological trap. We define 'adaptive' as not only allowing the animal immediate access to locally valued resources (Galef 1996) but also increasing the animal's long-term fitness. We define an ecological trap as a previously adaptive behaviour that has become maladaptive in a human-altered environment (Schlaepfer et al. 2002). For bears, gaining weight by exploiting sources of high-energy foods is adaptive. It is essential for overwinter survival and is correlated with both younger age of reproductive maturity and larger litters (Beckman & Berger 2003). When bears forage in developed areas, they obtain high-energy food, but in these human-altered environments, they are more likely to be hit by cars, hunted or killed because of safety concerns than are wild bears.

Female black bears appear to gain a few reproductive advantages from foraging in developed areas. In research done from 1974 to 1988 in Yosemite National Park, the time interval between litters of food-conditioned sows was 2.4 years versus 3 years in wild sows, but the difference was not significant (Keay 1990). There was no significant difference between the average litter size of wild sows and that of food-conditioned sows measured in 5-year intervals. In our study the same was true; food-conditioned sows produced more cubs than wild sows overall because we studied them longer, not because they had larger litters. For foraging in developed areas to be adaptive, the individual's fitness advantage of obtaining the high-energy human food would have to exceed the disadvantages of increased mortality. The reproductive advantage of food-conditioned foraging over wild foraging does not make up for this increased mortality. We found that once cubs of food-conditioned sows dispersed, they were then 5.6 times more likely to be killed because of their association with developed areas than were cubs of wild sows. Socially learned food-conditioned foraging therefore appears not to be an adaptive behaviour but, rather, may be leading bears into an ecological trap.

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References

- Beckman, J. P. & Berger, J. 2003. Using black bears to test ideal-free distribution models experimentally. *Journal of Mammalogy*, **84**, 594–606.
- Biossy, A. 1995. Fear and fearfulness in animals. *Quarterly Review of Biology*, **70**, 165–191.
- Boran, J. R. & Heimlich, S. L. 1999. Social learning in cetaceans: hunting, hearing and hierarchies. In: *Mammalian Social Learning: Comparative and Ecological Perspectives* (Ed. by H. O. Box & K. R. Gibson), pp. 282–307. Cambridge: Cambridge University Press.
- Caro, T. 1994. *Cheetahs of the Serengeti Plains: Group Living in an Asocial Species*. Chicago: University of Chicago Press.
- Caro, T. M. & Hauser, M. D. 1992. Is there teaching in nonhuman animals? *Quarterly Review of Biology*, **67**, 151–174.
- Dingemanse, N. J., Both, C., Drent, P. J., Van Oers, K. & Van Noordwijk, A. J. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, **64**, 929–938.
- Fragaszy, D. M. & Perry, S. 2003. Towards a biology of traditions. In: *The Biology of Traditions* (Ed. by D. M. Fragaszy & S. Perry), pp. 1–32. Cambridge: Cambridge University Press.
- Fragaszy, D. M. & Visalberghi, E. 1996. Social learning in monkeys: primate "primacy" reconsidered. In: *Social Learning in Animals: the Roots of Culture* (Ed. by C. M. Heyes & B. G. Galef, Jr), pp. 65–84. San Diego: Academic Press.
- Galef, B. G., Jr. 1977. Mechanisms for the social transmission of food preferences from adult to weaning rats. In: *Learning Mechanisms in Food Selection* (Ed. by L. M. Barker, M. Best & M. Domjan), pp. 123–150. Waco, Texas: Baylor University Press.
- Galef, B. G., Jr. 1996. Social enhancement of food preferences in Norway rats: a brief review. In: *Social Learning in Animals: the Roots of Culture* (Ed. by C. M. Heyes & B. G. Galef, Jr), pp. 49–64. San Diego: Academic Press.
- Galef, B. G., Jr & Giraldeau, L. A. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, **61**, 3–15.
- Galef, B. G., Jr & Laland, K. N. 2005. Social learning in animals: empirical studies and theoretical methods. *Bioscience*, **55**, 489–499.
- Gilbert, B. K. 1999. Opportunities for social learning in bears. In: *Mammalian Social Learning: Comparative and Ecological Perspectives* (Ed. by H. O. Box & K. R. Gibson), pp. 225–235. Cambridge: Cambridge University Press.
- Gittleman, J. L. 1986. Carnivore brain size, behavioral ecology, and phylogeny. *Journal of Mammalogy*, **67**, 23–36.
- Göth, A. & Evans, C. S. 2005. Life history and social learning: megapode chicks fail to acquire feeding preferences from conspecifics. *Journal of Comparative Psychology*, **119**, 381–386.
- Graber, D. M. & White, M. 1983. Black bear food habits in Yosemite National Park. *International Conference on Bear Research and Management*, **5**, 1–10.
- Griffin, A. S. & Evans, C. S. 2003. Social learning of antipredator behavior in a marsupial. *Animal Behaviour*, **66**, 485–492.
- Heyes, C. M. 1994. Social learning in animals: categories and mechanisms. *Biological Reviews*, **69**, 207–231.

- Keay, J.A.** 1990. Black bear population dynamics in Yosemite National Park. Ph.D. thesis, University of Idaho.
- Kitchener, A. C.** 1999. Watch with mother: a review of social learning in the Felidae. In: *Mammalian Social Learning: Comparative and Ecological Perspectives* (Ed. by H. O. Box & K. R. Gibson), pp. 236–258. Cambridge: Cambridge University Press.
- Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L. & Sherwin, W. B.** 2005. Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences, U.S.A.*, **102**, 8939–8943.
- Lee, D. J. & Vaughan, M. R.** 2003. Dispersal movements by subadult American black bears in Virginia. *Ursus*, **14**, 162–170.
- Lefebvre, L. & Giraldeau, L.** 1996. Is social learning an adaptive specialization? In: *Social Learning in Animals: the Roots of Culture* (Ed. by C. M. Heyes & B. G. Galef, Jr), pp. 107–128. San Diego: Academic Press.
- Matthews, S. M., Beecham, J. J., Quigley, H., Greenleaf, S. S. & Leithhead, H. M.** 2006. Activity patterns of American black bears in Yosemite National Park. *Ursus*, **17**, 30–40.
- Meagher, M. & Fowler, S.** 1989. The consequences of protecting problem bears. In: *Bear–People Conflicts: Proceedings of a Symposium on Management Strategies* (Ed. by M. Bromley), pp. 141–144. Yellowknife, Northwest Territories, Canada: Northwest Territories Department of Renewable Resources.
- Moore, B. R.** 1996. The evolution of imitative learning. In: *Social Learning in Animals: the Roots of Culture* (Ed. by C. M. Heyes & B. G. Galef, Jr), pp. 245–265. San Diego: Academic Press.
- National Park Service.** 1989. *Bear Management Plan*. Sequoia and Kings Canyon National Park, California: National Park Service.
- National Park Service.** 2001. *Black Bear Management and Incident Summary Report*. Yosemite National Park, California: National Park Service.
- National Park Service.** 2006. *Public Use Statistics Office*. Denver, Colorado: National Park Service Public Use Statistics Office. <http://www2.nature.nps.gov/stats>, accessed 01 April 2007.
- Nel, J. A. J.** 1999. Social learning in canidae: an ecological perspective. In: *Mammalian Social Learning: Comparative and Ecological Perspectives* (Ed. by H. O. Box & K. R. Gibson), pp. 259–278. Cambridge: Cambridge University Press.
- Page, R. & Ryan, M. J.** 2006. Social transmission of novel foraging behavior in bats: frog calls and their referents. *Current Biology*, **16**, 1201–1205.
- Perry, S.** 2003. Conclusions and research agendas. In: *The Biology of Traditions* (Ed. by D. M. Fragaszy & S. Perry), pp. 426–440. Cambridge: Cambridge University Press.
- Reader, S. M.** 2003. Innovation, social learning, and relative brain size in nonhuman primates. In: *The Biology of Traditions* (Ed. by D. M. Fragaszy & S. Perry), pp. 56–93. Cambridge: Cambridge University Press.
- Reale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemans, N. J.** 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews*, **82**, 291–318.
- Schlaepfer, M. A., Runge, M. C. & Sherman, P. W.** 2002. Ecological and evolutionary traps. *Trends in Ecology & Evolution*, **17**, 474–480.
- Sherry, D. F. & Galef, B. G., Jr.** 1984. Cultural transmission without imitation: milk bottle opening by birds. *Animal Behaviour*, **32**, 937–938.
- Stephenson, N.L.** 1988. Climate control of vegetation distribution: the role of the water-balance with examples from North America and Sequoia National Park, California. Ph.D. thesis, Cornell University.
- Terkel, J.** 1996. Cultural transmission of feeding behavior in the black rat (*Rattus rattus*). In: *Social Learning in Animals: the Roots of Culture* (Ed. by C. M. Heyes & B. G. Galef, Jr), pp. 17–47. San Diego: Academic Press.
- Thorpe, W. H.** 1963. *Learning and Instinct in Animals*. London: Methuen.
- West, M. J., King, A. P. & White, D. J.** 2003. Discovering culture in birds: the role of learning and development. In: *Animal Social Complexity: Intelligence, Culture, and Individualized Societies* (Ed. by F. B. M. de Waal & P. L. Tyack), pp. 470–492. Cambridge, Massachusetts: Harvard University Press.
- Whitehead, H.** 2003. Society and culture in the deep ocean: the sperm whale and other cetaceans. In: *Animal Social Complexity: Intelligence, Culture, and Individualized Societies* (Ed. by F. B. M. de Waal & P. L. Tyack), pp. 444–469. Cambridge, Massachusetts: Harvard University Press.
- Whiten, A. & Ham, R.** 2002. On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. *Advances in the Study of Behavior*, **21**, 239–283.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C.** 1999. Culture in chimpanzees. *Nature*, **399**, 682–685.