

Do woodpecker finches acquire tool-use by social learning?

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Tool-use is widespread among animals, but except in primates the development of this behaviour is poorly known. Here, we report on the first experimental study to our knowledge of the mechanisms underlying the acquisition of tool-use in a bird species. The woodpecker finch *Cactospiza pallida*, endemic to the Galápagos Islands, is a famous textbook example of tool-use in animals. This species uses modified twigs or cactus spines to pry arthropods out of tree holes. Using nestlings and adult birds from the field, we tested experimentally whether woodpecker finches learn tool-use socially. We show that social learning is not essential for the development of tool-use: all juveniles developed tool-use regardless of whether or not they had a tool-using model. However, we found that not all adult woodpecker finches used tools in our experiments. These non-tool-using individuals also did not learn this task by observing tool-using conspecifics. Our results suggest that tool-use behaviour depends on a very specific learning disposition that involves trial-and-error learning during a sensitive phase early in ontogeny.

Keywords: tool-use; social learning; ontogeny; Darwin's finches

1. INTRODUCTION

Tool-use is known from insects, mammals and birds (Beck 1980; Boswall 1977, 1983; Clayton & Jolliffe 1995; Hunt 1996; Van Lawick-Goodall & Van Lawick-Goodall 1966). Except for in primates, however, very little is known about its development. Social learning mechanisms, such as imitation, emulation, or local enhancement (Galef 1988; Moore 1992; Spence 1937; Thorpe 1956; Whiten & Ham 1992) have been assumed to be important in the acquisition of tool-use (Whiten *et al.* 1999). However, experimental support for social learning of tool-use exists only from a few studies of chimpanzees (Nagell *et al.* 1993; Tomasello *et al.* 1987; Whiten *et al.* 1996). Several studies indicate that social learning may also be an important mechanism in birds. It is a common mechanism in song learning (Marler 1991; Slater & Williams 1994), and it has been shown to affect the acquisition of specific feeding techniques (Fisher & Hinde 1949; Fritz & Kotschal 1999; Hellmann 1983; Palameta & Lefebvre 1985). Jones & Kamil (1973) suggested that a newly invented tool-use by Northern blue jays *Cyanocitta cristata* was transmitted socially to other jays. In contrast, the observation of one Egyptian vulture, *Neophron percnopterus*, showed that this individual developed stone-throwing in isolation (Thouless *et al.* 1987).

The woodpecker finch, belonging to the famous group of Darwin's finches, is endemic to the Galápagos Islands. Woodpecker finches use twigs or cactus spines, which they hold in their beaks, thus effectively extending their bodies, to push, stab or lever arthropods out of tree holes and crevices. This is not a stereotyped behaviour pattern, since woodpecker finches vary this technique according to the particular task. Moreover, they modify tools by shortening them when they are too long and break off twiglets that would prevent insertion (Eibl-Eibesfeldt 1961;

Millikan & Bowman 1967). Our field observations of woodpecker finches revealed that the frequency of tool-use clearly differs between habitats (Tebbich 2000). Tool-use occurs mainly in dry habitats where, especially in the dry season, prey is found under bark and is therefore hard to reach. There, 20 out of 21 individually identified woodpecker finches use tools and obtain 50% of their prey with this behaviour. By contrast, in humid habitats where woodpecker finches capture prey in moss and on leaves, tool-use occurs very rarely (Tebbich 2000).

Here, we present what we believe is the first experimental study of the influence of social learning on tool-use in birds. Specifically, we addressed the following questions. Firstly, do woodpecker finches of the humid zone vary in their ability to use tools? Secondly, do adult woodpecker finches that do not use tools learn this behaviour from a tool-using model? And finally, does the presence of a tool-using model influence the development of tool-use in young, naive birds?

2. METHODS

The study was carried out on Santa Cruz Island in the Galápagos Archipelago, Ecuador, during three field seasons: December 1995–April 1996; October 1996–April 1997; and January–May 1998.

(a) Tool-use abilities of adult birds

Twenty-eight woodpecker finches were mist-netted in the humid vegetation zone. After 4 days of habituation to the aviary, we tested their ability to recover food with the help of tools by presenting a beetle larva (*Euburnia* sp.) in an artificial tree trunk. This was a wooden block with a crevice (0.5 cm wide, 3 cm deep, 8 cm long, open on top and on one side). The prey was inaccessible without the help of tools. Ten twigs (2–15 cm in length) were put on the block and on the ground. Each test lasted 30 min. The tree trunk without prey and the tools were always in the aviary. Normal food was removed 1 hour before

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the experiment started. Individuals were tested singly, twice a day for 14 consecutive days. Frequency and duration(s) of behavioural categories (table 1) were recorded per 30 min with an event recording program, THE OBSERVER (Noldus Information Technology, Wageningen, The Netherlands).

(b) Social learning in adult birds

After testing the birds for their tool-using abilities, we placed 10 of the 15 non-tool-using individuals into the same cage with 10 tool-users. We put two wooden blocks and twigs in the aviary and repeated the same test procedure as described above for 14 more days. After this period with models, we tested the experimental birds again for their tool-use abilities for 4 days. The behaviour of models and test birds was recorded (frequency of visits to the trunk, probe with beak into the gap, tool manipulation and frequency and duration of tool-use).

(c) Social learning in young birds

We collected six broods and their parents from the humid zone 12 days after hatching. Woodpecker finches nest in closed, spherical nests, and therefore young cannot possibly see their parents using tools during the nestling phase. In two broods, we were able to catch both parents, and in four families only the male. Two broods consisted of three young, three broods of two young, and one brood consisted of one chick. Broods were first kept with their parents in a small cage (50 cm × 50 cm × 100 cm). Five days after fledging, young and parents were moved to an aviary (2 m × 2 m × 2 m) that contained only branches without bark, a gravel floor, and food and water. The birds were unable to use any of these materials to make tools. Next to the 'home aviary', there was a 'test aviary' (2 m × 2 m × 2 m) that was separated from the housing aviary by an opaque screen. The test aviary had branches, twigs, thorns, leaves, and two wooden blocks.

We split each brood with two or three chicks, assigning seven young to the test group in which each fledgling had a tool-using model, and their six siblings to the control group with non-tool-using models (figure 1). In the two broods with three chicks, two siblings were assigned to the same group. These siblings were treated as statistically independent, since none of the measured variables (table 2) was significantly correlated between siblings within each family (Spearman rank correlation: $r_s < 0.56$, $p > 0.5$, $n = 9$). The parents of the experimental young were tested over 14 days for their ability to use tools, as described above. Only two of the eight parents used tools, and therefore four juvenile test birds were exposed to an unrelated tool-user instead of a parental model. Juveniles did not respond more strongly to parental than to unrelated models. Instead, they tended to follow unrelated tutors more often (median = 5 occasions in all experiments, range 0–23, $n = 4$) than parents (median = 0.5, range 0–4, $n = 8$; Mann–Whitney U -test, $U = 6.5$, $p = 0.08$).

Each juvenile was placed in the test aviary twice a day for 15 min, once with a tool-using model (test group) or a non-tool-using model (control group), and once alone. The behaviour of both subjects was recorded continuously by direct observation and with the help of an event recorder. Every third day, the test without a model was additionally recorded on videotape. The development of one brood (F1 in figure 1, a single chick and its father) could not be recorded in sufficient detail. Therefore, we excluded this brood from all statistical comparisons between test and control groups.

Table 1. Behaviours of tool-using and non-tool-using adults, including staying on trunk and probing with beak into gap.

(Means and standard deviations are given for frequencies and durations (s) per test, $n = 10$ non-tool-using and 13 tool-using individuals (for five adults these behaviours were not recorded).)

behaviour	frequency, duration	tool-user	non-tool-user	p -value
on trunk	F	8.9 ± 4.9	6.8 ± 3.2	0.41 ^a
	D	193 ± 149	223 ± 174	0.61 ^b
probe	F	19.8 ± 26.0	23.7 ± 16.7	0.44 ^a

^aMann–Whitney U -test.

^b t -test.

3. RESULTS

(a) Do woodpecker finches vary in their ability to use tools?

Only 13 of the 28 adult woodpecker finches from the humid zone used tools in captivity during a five-week test period. Potential tools were available and the birds were highly motivated to extract prey that were presented in the artificial crevice. Motivation, measured as the number of visits to the experimental block, the duration of stay and the number of probes with the beak, did not differ between tool-using and non-tool-using individuals (table 1). The proportion of tool-using individuals did not differ between sexes ($n = 17$ males, 11 females, Fisher exact test: $p = 0.7$).

(b) Are adult woodpecker finches that do not use tools able to learn from a tool-using model?

We exposed 10 adult finches that had not used tools to a tool-using model for two weeks. Tool-using models used tools frequently (mean frequency ± s.d. = 6.2 ± 3.73 per test, mean duration ± s.d. = 184.8 ± 153.3 per test, $n = 10$). We recorded that non tool-using birds often observed the models, although our data do not permit any quantitative estimate of this behaviour. Before this exposure, 7 of the 10 woodpecker finches had never manipulated twigs, but three had picked up twigs and manipulated them. After the training period with a model, only 1 out of 10 finches successfully used tools. This was one of the three individuals that had already manipulated twigs before. The other nine birds tried, unsuccessfully, various other ways of reaching the prey, but they never paid any attention to the twigs.

(c) Does the presence of a tool-using model influence the development of tool-use in young, naive birds?

Juveniles interacted with their models and engaged in similar foraging behaviour (i.e. probing into substrate, pecking) as their models (6 cases with parents, 10 cases with unrelated models). Tool-using models performed tool-use frequently (mean ± s.d. = 10.6 ± 6.71 per test, $n = 6$), and two juveniles repeatedly took tools from the beaks of their models. However, the development of tool-use was not influenced by the presence of a tool-using

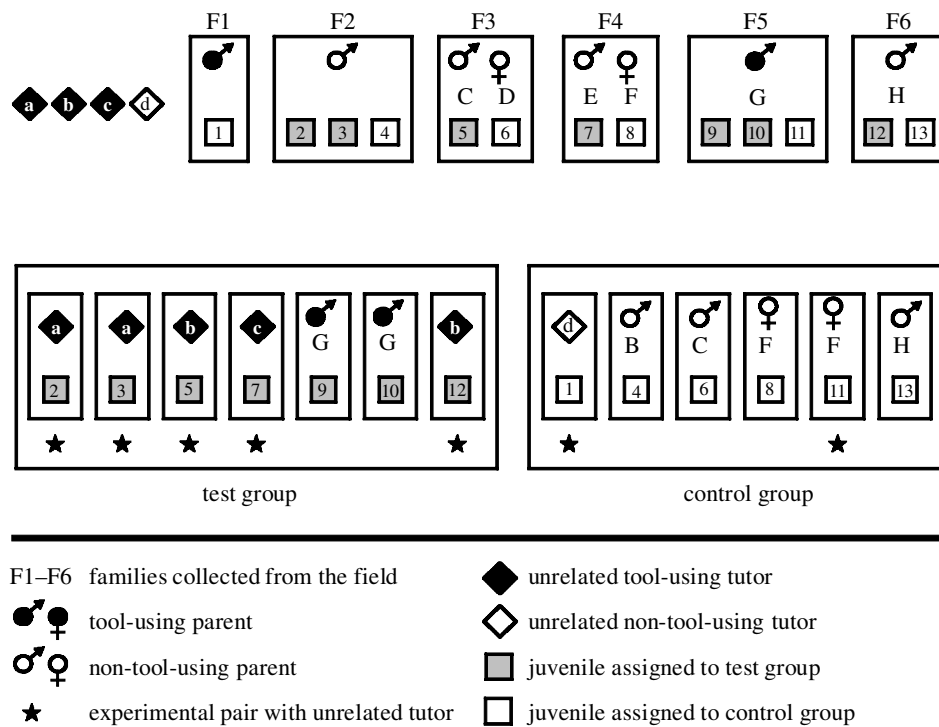


Figure 1. Assignment of juveniles, parents and unrelated tutors to test and control groups for examining the influence of a model on the development of tool-use in young, naive woodpecker finches.

model: all 13 young used tools after the five-week experimental period regardless of whether or not they had a model, and nine of them obtained prey successfully at least once with this technique. Five developmental steps characterized the acquisition of tool-use, with the onset of each step marked by the appearance of a new behaviour. The ages at which these steps were reached did not differ significantly between test and control groups (figure 2). Frequencies and duration of behaviours related to the trunk and the manipulation of twigs were similar between test and control groups. Only one behavioural parameter, watching the model, differed significantly between the test and control groups (table 2). During steps 2 to 5, juveniles showed tool manipulation that was not related to the prey. They turned the twigs around in exaggerated, playful movements using their beaks and feet.

Five individuals developed tool-use that differed from the typical form of this behaviour. They dropped the tool into the cavity and pulled it out with an upward motion of the beak. This movement levered the prey to within reach at the front of the crevice. In nature, where tool-use is mostly performed at tree holes, this technique of upward levering cannot be applied at these types of cavities. After the first success with this technique, the five birds used it significantly more often (total frequency before the first success, median = 1, range 0–5; after the first success, median = 11, range 4–21, Wilcoxon signed ranks test, $p = 0.043$), suggesting reinforced trial-and-error learning. Using the mean age at which the behaviour was first successful, the remaining unsuccessful birds showed no difference in frequency of tool-dropping before and after this age (before, median = 0, range 0–2; after, median = 0, range 0–1, Wilcoxon signed ranks test: $p = 0.3$; $n = 7$). These seven birds developed tool-use

Table 2. Behaviours of naive birds from test ($n = 6$) and control groups ($n = 6$).

(Behavioural categories include: stay on trunk; probe with beak into gap; pick up twig; manipulate twig; tool-use; success with tool-use; watch model; receive aggression from model. Means and standard deviations are given for frequencies and durations (s) per test. Except when comparing tool-use, for which the Mann-Whitney U -test was used, t -tests were performed.)

behaviour	frequency, duration	test	control	p -value
on trunk	F	6.3 ± 2.2	6.7 ± 2.4	0.81
	D	353 ± 164	302 ± 57	0.49
probe	F	19.7 ± 7.0	20.3 ± 10.5	0.91
	F	7.7 ± 2.1	10.7 ± 5.5	0.25
manipulate	F	7.4 ± 1.7	10.7 ± 6.7	0.28
	D	127 ± 45	154 ± 102	0.57
tool-use	F	3.6 ± 2.3	5.6 ± 5.3	0.52
	D	48 ± 70	61 ± 51	0.08
success	F	0.83 ± 0.75	0.94 ± 0.92	0.83
watch	F	5.4 ± 1.7	2.4 ± 0.7	0.005
	D	109 ± 77	40 ± 13	0.08
aggression	F	2.6 ± 1.8	1.4 ± 1.3	0.21

without this behaviour being reinforced by obtaining prey.

4. DISCUSSION

Our study shows that social learning is not essential for the development of tool-use in the woodpecker finch. Not all woodpecker finches from the humid zone used tools in our experiments, but probably these differences cannot be

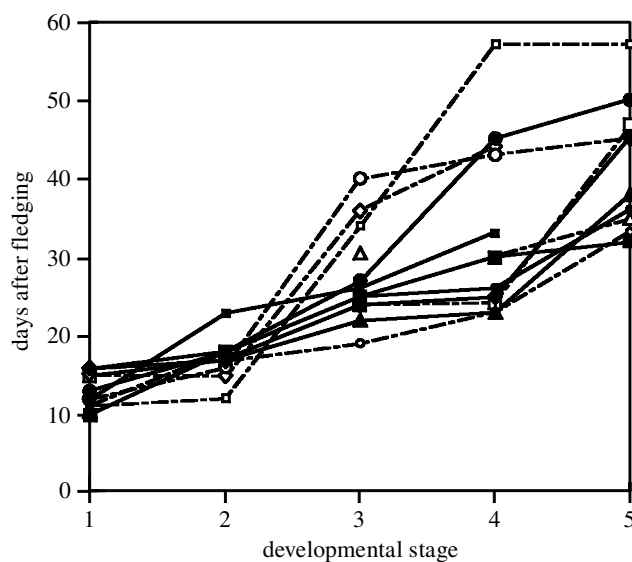


Figure 2. Development of tool-use behaviour in six juveniles with a tool-using model (solid lines) and six juveniles with a non-tool-using model (dot-dashed lines). The symbols represent different individuals. Birds of the two groups did not differ in age at which they reached the five successive developmental steps, which were as follows: (i) biting the end of twigs on bushes ($t = -0.247$, $p = 0.81$); (ii) horizontal and vertical manipulation of twigs in the beak ($t = -2.101$, $p = 0.06$); (iii) uncoordinated manipulation of twigs near the crevice, sometimes dropping them into it ($t = 1.419$, $p = 0.21$); (iv) vertical insertion of twigs into the crevice ($t = 1.018$, $p = 0.34$); (v) tool-use involving pushing or levering the larvae ($n = 5 + 5$, $t = -0.580$, $p = 0.59$).

attributed to spatial patterns of social transmission, as found in chimpanzees (Whiten *et al.* 1999). We found that adult finches that did not use tools also did not learn tool-using from tool-using conspecifics. Only one non-tool-using adult used tools after exposure to a model. Since this individual had manipulated twigs already before the exposure, its success does not necessarily indicate social learning. Rather, this may represent social enhancement of an already existing behavioural pattern (Galef 1988; Thorpe 1956) and a conservative interpretation of our results is therefore demanded. Our experiments with young, naive finches show that the presence of a model does not influence the ontogeny of tool-use: this behaviour was expressed in the absence of a model and the development was not slower without than with a model. In the latter analysis, sample sizes were small, resulting in low statistical power. With one exception, however, all differences were far from being significant. There was a tendency in one test ($p = 0.06$), but in this case juveniles without a model showed faster development than those with models.

No behaviour has exclusively learned or innate components (Shettleworth 1998). The aim of this study was not to quantify the relative influence of genes and environment on the development of tool-use behaviour, but our data suggest that both factors may be important. All juveniles showed a similar pre-functional development of tool-use, and seven juveniles developed tool-use without being reinforced by receiving prey. This indicates that this is a species-typical behaviour that matures. However,

this does not exclude the influence of learning processes and practice (Oyama 1982). The undirected playful manipulation of twigs could help to improve coordination, as it could enhance cerebellar synaptogenesis (Byers & Walker 1995). Playful manipulation of tools is characteristic of most juvenile primates with tool-using abilities (Beck 1972, 1973, 1976; Glickman & Sroges 1966; Parker 1974). Brown-capped cebus monkeys, *Cebus apella*, are only effective in tool-use when engaged in intensive playful manipulations of tools before (Parker & Poti 1990). Our observations on the non-typical tool-use suggest that woodpecker finches learn by trial-and-error. This may be important for achieving the fine-tuned motor coordination found in adults.

Our conclusion that the development of tool-use is not entirely under genetic control is further supported by the difference in tool-use between parents and their young: only two out of six parents used tools, whereas all of their 13 young did. In the two complete families, none of the four parents showed tool-use, but all four young developed this behaviour. This result suggests an important environmental influence on the development of tool-use. Specifically, parents and young were most probably exposed to different environmental conditions in their early development. In captivity, parents and their young had equal opportunities to develop tool-use. All parents came from the humid zone, however, where tool-use is not necessary and probably also constrained by the lack of tree holes (Tebich 2000). Thus, the behavioural difference between juveniles and adults found in our experiments may be explained by a sensitive phase during ontogeny at which tool-use must be learned. Tool-use in primates and the acquisition of special feeding techniques in birds and mammals suggest similar age effects (Byrne & Byrne 1993; Vince 1958; Watanabe 1994; Westergaard *et al.* 1998; Zohar & Terkel 1996). An alternative explanation may be that parents had acquired tool-use in their ontogeny, but lost this ability later in life because, with the easy accessibility of prey in the humid zone, tool-use was insufficiently reinforced.

In summary, we found no evidence that woodpecker finches, in contrast to chimpanzees, learn tool-use socially. Rather, they seem to have a specific learning disposition that involves trial-and-error learning during a sensitive phase. For woodpecker finches in the arid zone, tool-use seems to be essential, especially in the dry season (Tebich 2000). The specific learning predisposition for tool-use, suggested by our results, ensures that this important feeding technique is part of the behavioural repertoire, but also that it is open to modification. Recent research in navigation (Able & Able 1999), song learning (Marler 1999) and memory (Sherry 1999) supports the idea that a genetic disposition for a specific learning processes may be useful for behavioural adaptations to variable environments.

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REFERENCES

- Able, P. A. & Able, A. A. 1999 Migratory orientation: learning rules for a complex behaviour. In *Proc. 22 Int. Ornithol. Congr., Durban, 1998* (ed. N. J. Adams & R. H. Slotow), pp. 2356–2365. Johannesburg: BirdLife South Africa.
- Beck, B. B. 1976 Tool use by captive pigtailed macaques. *Primates* **17**, 301–310.
- Beck, B. B. 1980 *Animal tool behavior: the use and manufacture of tools by animals*. New York: Garland STPM Press.
- Beck, B. B. 1972 Tool use in captive hamadryas baboons. *Primates* **13**, 276–296.
- Beck, B. B. 1973 Observation learning of tool use by captive Guinea baboons (*Papio papio*). *Am. J. Phys. Anthropol.* **38**, 579–582.
- Boswall, J. 1977 Tool-using by birds and related behaviour. *Avic. Mag.* **83**, 146–159.
- Boswall, J. 1983 Tool-using and related behaviour in birds: yet more notes. *Aviculture Mag.* **89**, 170–181.
- Byers, J. A. & Walker, C. 1995 Refining the motor training hypothesis for the evolution of play. *Am. Nat.* **146**, 25–40.
- Byrne, R. W. & Byrne, J. M. E. 1993 Complex leaf-gathering skills of mountain gorillas (*Gorilla g. beringei*): variability and standardization. *Am. J. Primatol.* **31**, 241–261.
- Clayton, N. S. & Jolliffe, A. 1995 Marsh Tits *Parus palustris* use tools to store food. *Ibis* **138**, 554.
- Eibl-Eibesfeldt, I. 1961 Über den Werkzeuggebrauch des Spechtfinke *Camarhynchus pallidus* (Slater und Slavín). *Z. f. Tierpsychol.* **18**, 343–346.
- Fisher, J. & Hinde, R. A. 1949 The opening of milk bottles in birds. *British Birds* **42**, 347–357.
- Fritz, J. & Kotschal, K. 1999 Social learning in common ravens *Corvus corax*. *Anim. Behav.* **57**, 785–793.
- Galef, B. G. 1988 Imitation in animals: history, definition, and interpretation of data from the psychological laboratory. In *Social learning: psychological and biological perspectives* (ed. T. R. Zentall & B. G. Galef), pp. 3–28. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Glickman, S. & Sroges, R. 1966 Curiosity in zoo animals. *Behaviour* **26**, 151–188.
- Hellmann, R. 1983 Observational learning in blue tits. *Naturwissenschaften* **70**, 260.
- Hunt, G. R. 1996 Manufacture and use of hook-tools by Caledonian crows. *Nature* **379**, 249–251.
- Jones, T. B. & Kamil, A. C. 1973 Tool-making and tool-using in the northern blue jay. *Science* **180**, 1076–1077.
- Marler, P. 1991 The instinct to learn. In *The epigenesis of mind: essays on biology and cognition* (ed. S. Carey and R. Gelman), pp. 37–66. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Marler, P. 1999 Nature, nurture and the instinct to learn. In *Proc. 22 Int. Ornithol. Congr., Durban, 1998* (ed. N. J. Adams & R. H. Slotow), pp. 2353–2355. Johannesburg: BirdLife South Africa.
- Millikan, G. C. & Bowman, R. I. 1967 Observations on Galápagos tool-using finches in captivity. *Living Bird* **6**, 23–41.
- Moore, B. R. 1992 Avian movement imitation and a new form of mimicry: tracing the evolution of a complex form of learning. *Behaviour* **122**, 231–263.
- Nagell, K., Olguin, R. S. & Tomasello, M. 1993 Processes of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *J. Comp. Psychol.* **107**, 174–186.
- Oyama, S. 1982 A reformulation of the idea of maturation. In *Perspectives in ethology* (ed. P. P. G. Bateson & P. H. Klopfer), pp. 101–131. New York: Plenum Press.
- Palameta, B. & Lefebvre, L. 1985 The social transmission of a food-finding technique in pigeons: what is learned? *Anim. Behav.* **33**, 892–896.
- Parker, C. 1974 Behavioral diversity in ten species of nonhuman primates. *J. Comp. Psychol.* **87**, 930–937.
- Parker, S. T. & Poti, P. 1990 The role of innate motor patterns in ontogenetic and experimental development of intelligent use of sticks in cebus monkeys. In *'Language' and intelligence in monkeys and apes* (ed. S. T. Parker & K. R. Gibson), pp. 219–243. Cambridge University Press.
- Sherry, D. F. 1999 Adaptive specialisations of memory in birds. In *Proc. 22 Int. Ornithol. Congr., Durban, 1998* (ed. N. J. Adams & R. H. Slotow), pp. 2394–2416. Johannesburg: BirdLife South Africa.
- Shettleworth, S. 1998 *Cognition, evolution, and behavior*. New York: Oxford University Press.
- Slater, P. J. B. & Williams, J. M. 1994 Bird song learning: a model of cultural transmission? In *The ethological roots of culture*, vol. 78 (ed. R. A. Gardner, B. T. Gardner, B. Chiarelli & F. X. Plooj), pp. 95–106. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Spence, K. W. 1937 Experimental studies of learning and higher mental processes in infra-human primates. *Psychol. Bull.* **34**, 806–850.
- Tebbich, S. 2000 Tool-use in the woodpecker finch *Cactospiza pallida*: ontogeny and ecological relevance. PhD thesis, University of Vienna, Austria.
- Thorpe, W. H. 1956 *Learning and instinct in animals*. London: Methuen & Co. Ltd.
- Thouless, C. R., Fanshawe, J. H. & Bertram, C. R. 1987 Egyptian Vultures *Neophron percnopterus* and Ostrich *Struthio camelus* eggs: the origins of stone-throwing behaviour. *Ibis* **131**, 9–15.
- Tomasello, M., Davis-Dasilva, M. & Camak, L. 1987 Observational learning of tool-use by young chimpanzees. *Hum. Evol.* **2**, 175–183.
- Van Lawick-Goodall, J. & Van Lawick-Goodall, H. 1966 Use of tools by the Egyptian vulture, *Neophron percnopterus*. *Nature* **212**, 1468–1469.
- Vince, M. A. 1958 'String pulling' in birds. Differences related to age in greenfinches, chaffinches and canaries. *Anim. Behav.* **6**, 53–59.
- Watanabe, K. 1994 Precultural behavior of Japanese macaques: longitudinal studies of the Koshima troops. In *The ethological roots of culture*, vol. 78 (ed. R. A. Gardner, B. T. Gardner, B. Chiarelli & F. X. Plooj), pp. 81–94. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Westergaard, G. C., Lundquist, A. L., Haynie, M. K., Kuhn, H. E. & Suomi, S. J. 1998 Why some capuchin monkeys (*Cebus apella*) use probing tools (and others do not). *J. Comp. Psychol.* **112**, 207–211.
- Whiten, A. & Ham, R. 1992 On the nature and evolution of imitation in the animal kingdom: reappraisals of a century of research. *Adv. Study Behav.* **21**, 239–283.
- Whiten, A., Custance, D. M., Gomez, J.-C., Teixidor, P. & Bard, K. A. 1996 Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **110**, 3–14.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T. & Reynolds, V. 1999 Culture in chimpanzees. *Nature* **399**, 682–685.
- Zohar, O. & Terkel, J. 1996 Social and environmental factors modulate the learning of pine-cone stripping techniques by black rats, *Rattus rattus*. *Anim. Behav.* **51**, 611–618.