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Social learning and innovation are positively correlated in pigeons (*Columba livia*)

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Abstract When animals show both frequent innovation and fast social learning, new behaviours can spread more rapidly through populations and potentially increase rates of natural selection and speciation, as proposed by A.C. Wilson in his behavioural drive hypothesis. Comparative work on primates suggests that more innovative species also show more social learning. In this study, we look at intra-specific variation in innovation and social learning in captive wild-caught pigeons. Performances on an innovative problem-solving task and a social learning task are positively correlated in 42 individuals. The correlation remains significant when the effects of neophobia on the two abilities are removed. Neither sex nor dominance rank are associated with performance on the two tasks. Free-flying flocks of urban pigeons are able to solve the innovative food-finding problem used on captive birds, demonstrating it is within the range of their natural capacities. Taken together with the comparative literature, the positive correlation between innovation and social learning suggests that the two abilities are not traded-off.

Keywords Social learning · Innovation · Pigeons

Introduction

Novel feeding behaviours can originate in animals through two non-genetic means: social learning and individual innovation. Broadly defined, social learning is a change in the behaviour of one animal that results from paying attention to the behaviour of another (Fragaszy and Perry 2003). There is a large body of literature on olfactory (Galef 1996) and visual (Heyes and Galef 1996) modes of social learning of new food types and new foraging techniques in vertebrates (e.g. birds: Lefebvre and Bouchard 2003; primates: Reader and Laland 2002) and invertebrates (Webster and Fiorito 2001), with classical cases like bottle opening in English tits dating back to the 1920s (Fisher and Hinde 1949). Much more recent is the study of animal innovation, the invention of a new behaviour pattern or the modification of an old one in a novel context (Reader and Laland 2003). Studies of innovation have only been conducted in the past two decades (Kummer and Goodall 1985; Lefebvre et al. 1997) and the first and only textbook in this area dates from 2003 (Reader and Laland 2003).

As a consequence, the relationship between innovation and social learning is not well understood, despite its importance in the primary model on the role of cognition in evolution, A.C. Wilson's behavioural drive hypothesis (Wyles et al. 1983; Wilson 1985). All other things being equal, opportunistic, large-brained animals that innovate more frequently or acquire new behaviours by observing others will come into more frequent contact with environmental conditions likely to provide a selective context for randomly occurring mutations. For example, a mutation in the enzymes that would allow a bird to digest lactose (birds digest the lipids in milk, not the carbohydrates; Martinez del Rio 1993) might provide a tit with a reproductive advantage over nonmutants, but would disappear with its bearer if it occurred in a conservative, small-brained species that never innovated or copied milk-bottle opening.

To date, only four studies have tested this idea. Wyles et al. (1983) found faster rates of anatomical evolution in larger-brained taxa like passeriformes and mammals, compared to smaller brained clades like amphibians and reptiles.

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Nicolakakis et al. (2003) reported a higher rate of species diversification in avian parvorders that are larger-brained and have a higher rate of innovation. Sol et al. (2005) showed that larger-brained species of Holarctic Passeriformes have more subspecies. In a study of 116 primate species, Reader and Laland (2002) provided empirical support for one of the key assumptions of behavioural drive, positive correlations between the taxonomic distribution of innovation rate, relative neocortex size and rate of social learning.

No study has yet examined the correlation between innovation and social learning at the intra-specific level. This is the goal of the present study. We presented feral pigeons with two tasks previously used to assess innovation and social learning in birds. Innovative problem solving can be assessed by a bird's readiness to open a closed container with visible food that can be reached through a variety of manipulanda requiring pecking, pushing, lifting or pulling actions. This task has been shown to discriminate well between five Passeriforme and Columbiforme species both in captivity and in the field in the West Indies, suggesting it is within the range of their natural behaviour (Webster and Lefebvre 2001). Taxonomic differences on the task correlate closely with how frequently birds from the five taxa show feeding innovations in the field (Lefebvre and Bolhuis 2003).

The second task has been used in several studies of social learning on pigeons (Giraldeau and Lefebvre 1987; Giraldeau and Templeton 1991). The design involves an apparatus containing hidden food that naïve, hungry pigeons cannot find on their own (control pre-test). A shaped bird then performs an apparatus-opening technique in front of the naïve observer, which is then tested with the closed apparatus in the absence of the demonstrator. The latency to first opening of the apparatus is a measure of social learning, all subsequent openings benefiting from personal information about the apparatus. This design can only test for generic social learning and does not discriminate between the possible mechanisms (imitation, stimulus enhancement, goal emulation) that underlie learning in this situation.

There are three possible relationships between the performances of individual birds on the two tasks. First, if both innovation and social learning are rapid in some individuals and absent or slow in others, this should result in a positive correlation between performances on the two tasks. In such a case, it is important to show that a common variable like willingness to search for food in an unfamiliar apparatus is not affecting both tasks and spuriously causing the positive relationship. We therefore add a control task to our study, Greenberg's (1984, 1990) standard test for object neophobia during feeding tasks. Originally conceived to measure differences between generalist and specialist species, the test has proven useful in teasing out the factors that affect performance on cognitive tests (Seferta et al. 2001). We also recorded sex and priority of access to a defendable feeder, to see if an eventual positive correlation between social learning and innovation is due to a common effect of gender or dominance status (Reader and Laland 2001). If either males or females and dominants or subordinates more rapidly interact with feeding situations, this may create a spurious positive correlation between performance on the social and innovation tasks.

The second possible correlation is a negative one. This can occur if the memory systems for the cognitive abilities are traded-off (Sherry and Schacter 1987; Shettleworth 1998). It can also occur if birds adopt stable producer–scrounger tactics, where a part of the population searches for its own new feeding opportunities and another part uses the searching behaviour of the producers (Giraldeau and Caraco 2000). Good social learners thus exploit good innovators in this system, which might depend on frequency-dependent payoffs. Frequency-dependence is known to limit the spread of new behaviours (Giraldeau and Caraco 2000), so that a negative relationship might slow down behavioural drive by decreasing the rate at which the average bird encounters environmental conditions likely to select for a mutation.

The third possible relationship is a zero or non-significant correlation between performances on the two tasks, which would imply that the processes behind them are independent. These are the three hypotheses we contrast in an experiment on captive pigeons. To make sure that our results are not artefacts of captive conditions, we also test flocks of urban pigeons on the innovation task, social learning being impossible to distinguish from individual learning in the uncontrolled setting of the field (Lefebvre 1986). Cognitive tasks that force a food-deprived animal housed alone in a cage to interact with an unfamiliar apparatus may have questionable validity. If the task can be solved by animals in the field, under normal conditions of hunger, social interactions and feeding options other than the one offered by the apparatus, we can be more confident that it assesses abilities animals use in their usual environment.

Methods

Subjects

Forty-four adult, wild-caught feral pigeons were obtained from a commercial dealer (Stephen Wright, Richmond Hill, Ontario). Two birds were randomly chosen to be shaped as demonstrators for the social learning test and remained in the laboratory for the whole 6-month period. The remaining 42 birds (in three groups of 12 and one group of six) were subjected to a series of tests over a period of 4 weeks each in 2001.

Upon reception, all birds were identified with a coloured plastic leg band, and housed in single

43 cm \times 53 cm \times 30 cm cages. They had ad libitum access to water and grit at all times, and to a commercial seed mix for a minimum of 2 days. The birds were then weighed, and the amount of food given to them was carefully controlled on subsequent days to progressively bring all individuals down to 85–90% of their ad libitum weight for the experimental period. Once birds had reached their target deprivation weight, testing began. Before each testing day, the subjects were food deprived for 18 h overnight, and then moved from the housing room to the experimental room where they were given a 10 min habituation period. During all tests, the experimenter was hidden behind a blind and observed the birds' behaviours using a closed-circuit video system.

We presented each subject with a series of four tests: neophobia, innovation, social learning, and priority of access to food. We chose to keep the order of tests constant (as in Whittle 1996; Seferta et al. 2001; Webster and Lefebvre 2001) because a gradual habituation to novel stimuli and captivity as testing proceeds could potentially mask any association between social learning and innovation if the order of these tests were counterbalanced or randomised. For example, if gradual habituation occurred, birds tested first on innovation would do poorly on that test, and better on the social learning test; birds given the tests in the opposite order would show the reverse pattern, creating a spurious negative correlation between social learning and innovation (Beauchamp personal communication).

Neophobia tests

The neophobia test followed the procedure designed by Greenberg (1983), and compared the latency to feed in trials randomly featuring either a novel object or no novel object (control) placed next to a food dish. We conducted the neophobia test over 3 consecutive days (two trials per day, 2 h apart), with three novel object and three control trials, for a total of six trials. Each day, we randomly determined if the novel object or the control trial would be presented first; the

second trial that day then involved the opposite condition. During an experimental trial, subjects were given 20 g of mixed seeds in their usual feeding dish, and latency to initiate feeding was recorded (in seconds). If they did not feed within 20 min, the trial was ended and another trial was attempted later that day or on a subsequent day. Once the birds had fed for 5 s, the experimenter slowly approached the cage, opened the door, and placed one of five novel objects 2 cm away from the food dish. The experimenter then backed away and returned behind the blind. We recorded the latency to resume feeding after the introduction of the novel object. If an individual did not feed within 20 min, we recorded a ceiling latency of 1201 s. The novel objects were made of artificial materials and unusual man-made items to minimise the probability that subjects had encountered them in the past (Greenberg 1990). We determined the order of presentation of these objects randomly. We conducted control trials exactly like novel object trials, but instead of introducing a novel object, the experimenter put one hand in the cage for 3 s. To yield neophobia levels for each individual, latencies to feed in control trials were averaged and subtracted from mean latency to feed in novel object trials.

Innovation test

We used the apparatus designed by Webster and Lefebvre (2001; see their Fig. 1) to assess innovative problem-solving ability. A clear Plexiglas box (18 cm \times 6.5 cm \times 4.5 cm) was filled with the birds' usual seed mix. The birds could open the box and obtain seeds by pulling or pushing the middle drawer, pulling the two end drawers, or removing the two lids; each lid and drawer was fitted with a metal ring. We placed the box in the centre of the birds' home cages for a single 30 min trial, and recorded the latency to open the box with the beak (modified from Webster and Lefebvre 2001). If an individual did not open the box, we recorded the ceiling latency of 1801 s. Birds were carefully monitored for accidental openings with the wings or feet, but this never occurred.

Fig. 1 The relationships between **A** social learning and innovation, and **B** residual social learning and residual innovation, both regressed against neophobia. Low values indicate fast social learning and/or innovation; high values indicate slow social learning and/or innovation



Social learning test

We shaped two demonstrators to remove the stopper from an inverted, opaque, test tube containing 0.5 g of mixed seeds. The stopper was fitted with a wooden tab that the pigeons could peck or grasp with the bill and twist in a downward motion to release the seeds into their food dish (see Giraldeau and Lefebvre 1987 for a description of the task). Demonstrators were considered efficient when they could routinely open the test tube in less than 5 s after presentation of the apparatus. Before the social learning test, the subjects were transferred to smaller 23 cm \times 38 cm \times 28 cm cages in which all sides were opaque except the door in the front. These cages had the advantage of offering very few distractions and ensured that the birds were facing the door most of the time. A 20 cm \times 5 cm hole in the door allowed the birds access to the apparatus. A control trial was performed prior to the social learning test: the apparatus was placed in front of each individual for 20 min to control for spontaneous opening; no birds opened during this period.

Social learning trials were conducted over a 4-day period, at the rate of five trials per day. The cages of the demonstrator and the naïve observer were placed on the floor, 40 cm apart, and positioned so that they faced each other at a 45° angle. Before each trial, the inverted test tube was first presented to the demonstrator, who rapidly removed the stopper and released the seeds into its food dish. After the demonstrator had fed for 10 s, a blind was placed between the two cages to avoid social facilitation effects, and the test tube was presented to the observer for a 1 min trial. If the observer succeeded in removing the stopper within this 1 min period, it received 0.5 g of mixed seeds delivered to its food dish via a section of plastic tubing. The observers' test tubes were always empty to avoid rewarding accidental openings (e.g. with the head or the back of the neck while trying to escape). If the observer did not succeed, another demonstration-trial cycle was performed 1 min later, up to a maximum of five trials per day. We recorded the number of trials required by each individual to learn the task as the measure of social learning ability. If an individual did not learn to open the test tube within the 20 trials, the ceiling value of 21 was recorded.

Determining sex and priority of access to food

After the neophobia, innovation and social learning tests, we examined two variables that might account for an eventual correlation between social learning and innovation: sex and priority of access to food. Forty randomly chosen pigeons (of the 42 used in the previous tests) were placed in $0.9 \text{ m} \times 1.4 \text{ m} \times 2.3 \text{ m}$ aviaries in groups of four. After a 6–7 day familiarisation period, two trials of the priority of access to food test were performed on the same day, 2 h apart. The

apparatus consisted of a large cylinder (height: 15 cm, diameter: 3.5 cm) filled with mixed seeds, with a small opening at the bottom such that only one pigeon could feed at any given moment (Giraldeau and Lefebvre 1987). The cylinder was placed on the floor, in the centre of the aviary, for two 10 min trials. The amount of time spent feeding by each bird was recorded. Each individual was then ranked (1–4) according to how much time it spent feeding compared to its three companions (1 = most feeding time, 4 = least feeding time). The sex of most individuals (N = 36) was determined by a combination of cloacal examination and behavioural observations of displays while grouped in aviaries.

We log transformed ($\log_{10}[x + 1]$) the innovation, social learning and neophobia variables collected during the captive study because of non-normal distributions, and thus were able to use parametric statistical procedures. All statistical tests used were two-tailed tests.

Validating the innovation task in the field

Free-living urban pigeons at 12 sites on the island of Montreal served as subjects for the field experiments in the summer of 2001. Distance between the sites ranged from 0.4 to 6.4 km, with an average of 2.2 km. Flock size varied from seven to 175 pigeons depending on the site, but day-to-day fluctuations in numbers for a given site were minimal. For 2 days before the tests began, we visited each site at a specific time and offered 50 g of mixed seeds at the feeding area to habituate the pigeons to the time and place of feeding. On subsequent days, we presented the Plexiglas box used in the captive innovation test at each site for a maximum of two 20 min trials over 2 consecutive days. Latencies to first contact and to successful opening of one of the lids or drawers were taken from the video records of each trial, as well as flock size. When no birds opened the box or when the opening could have been accidental, we assigned the maximum latency of 2402 s to this flock. To analyse the results from the field tests, we used non-parametric statistics, as no transformation could correct for the non-normal distributions of the data.

Results

In the field, eight of the 12 flocks opened the Plexiglas box; in two of these cases, we could not exclude that the first opening was accidental. Of the four flocks that did not open the box, two made contact with it. Latency to first opening of the box was positively correlated with latency to first contact and flock size, but these correlations fell short of the 0.05 significance threshold (first contact: Spearman *rho*: 0.549, P = 0.064, n = 12; flock size: *rho*: -0.560, P = 0.051, n = 12).





In captivity, performances on the innovative problemsolving and social learning tasks were strongly correlated (r = 0.740, n = 42, P < 0.001; Fig. 1A); individuals that solved the Plexiglas box problem quickly also learned readily from a demonstrator, and vice-versa. More importantly, when innovation and social learning were regressed separately against neophobia to remove the effect of this intervening variable, their residuals remained significantly correlated (r = 0.709, n = 42, P < 0.001; Fig. 1B). Neophobia was associated with both social learning (r = 0.344, n = 42, P = 0.026; Fig. 2A) and innovation (r = 0.312, n = 42, P = 0.044; Fig. 2B). In other words, individuals with low neophobia learned and innovated more quickly than individuals whose neophobia levels were higher.

In the neophobia test, mean latency to resume feeding after interruption by the experimenter was significantly higher in novel object trials than in control trials (paired *t* test: $t_{41} = -11.645$, P < 0.001), indicating that novel objects elicited fear beyond that caused by the interruption. Moreover, when individuals where tested again with an object they had previously seen, their latency to feed quickly decreased to zero. This further confirms that the birds were reacting to the novelty of the objects, rather than to their presence.

In the innovation test, 35 of 42 subjects were successful in opening and feeding from the Plexiglas box. Mean latency to opening was 758 s (SEM = 107). For each successful opening, the individuals were clearly seen deliberately opening the box in one of three ways: (1) picking up a lid with the beak, (2) pecking on a drawer to make it slide out of the box, (3) pushing a lid with the foot. When individuals were given subsequent opportunities to feed from the box, they always opened it using the same method as their first successful opening, showing that the innovative behaviour was learned and maintained.

Of the seven that did not succeed, four did contact the box during the 30 min trial. No subject solved the social learning task during the 20 min control trial for spontaneous opening. Of the 42 pigeons tested, only seven failed to learn the task after watching 20 demonstrations, and of those seven, four were not successful in the innovation task either. The mean number of trials to opening was 10.45 (SEM = 1.04).

In accordance with previous studies on pigeons (e.g. Giraldeau and Lefebvre 1987), sex did not affect performance of individuals on the neophobia (ANOVA: $F_{1,34} = 2.352$, P = 0.134), innovation ($F_{1,34} = 2.696$, P = 0.110) or social learning tests ($F_{1,34} = 0.464$, P = 0.501), and there were no significant differences in performance on the three tests in birds with different ranks on the priority of access to food test (neophobia: $F_{1,34} = 1.693$, P = 0.186; innovation: $F_{1,34} = 1.226$, P = 0.314; social learning: $F_{1,34} = 0.962$, P = 0.421).

Discussion

Three main conclusions can be drawn from this study. First, performance on the innovation and social learning tasks we used clearly co-varies in pigeons. Subjects that opened the Plexiglas box quickly were also the more successful ones when learning from a demonstrator. Second, the positive association between innovation and social learning was not due to the confounding effect of neophobia. Performances on both the innovative problem-solving task and the social learning task were associated with fear of novel stimuli in captivity, confirming the importance of this variable in cognition (Greenberg 1983). When the effect of neophobia on each variable was removed, however, innovative problem-solving and social learning remained significantly correlated. This suggests that neophobia and whatever non-neophobic measure of cognition is expressed by our residuals are independent components of performance on learning tasks. Finally, the innovative problem-solving test in the field validated the captive test; free-living pigeons were also able to open the Plexiglas box, confirming that opening in captivity could not solely be attributed to features of the testing situation such as food deprivation, lack of alternative feeding options and forced proximity to the apparatus. Taken together, our results support the assumptions of the behavioural drive hypothesis, according to which the co-occurrence of innovativeness and

social learning is a pre-requisite for the potentially accelerating effect of cognition on evolutionary rate.

It is obviously impossible to eliminate all the confounding variables that could influence the positive correlation between social learning and innovation. Our conclusion that there is no trade-off (caused, for example by limited memory or fixed innovator-copier roles) between the abilities measured here is thus a tentative one, subject to confirmation by future work. The conclusion is nevertheless consistent with all but one study comparing social and individual routes to the adoption of new feeding techniques. Reader and Laland's (2002) work on 116 primates, Sasvári's (1985a,b) work on five passerines, Whittle's (1996; reanalysed by Seferta et al. 2001) experiments on two finch species and Lefebvre et al.'s (1996) work on two Columbiformes all yield a positive correlation between social learning and either individual innovation or learning (reviewed by Lefebvre and Giraldeau 1996). Lefebvre and Bolhuis (2003) and Lefebvre et al. (2004) further show positive correlations between innovation rate, tool use rate, learning performance and relative size of association areas in the brain in both birds and primates.

Although the relationship between innovation and social learning persists when we remove the common effects of neophobia, it is possible that other individual differences underlie the correlation. A growing literature suggests that many behavioural traits that vary consistently between individuals are manifested (and probably selected, Both et al. 2005; Dingmanse and Réale 2005) as syndromes (reviewed by Sih et al. 2004). In tits, the speed with which individuals explore new situations shows long-term correlations with social and agonistic behaviours (Carere et al. 2005). In geese, innovativeness in feeding tests may also be part of a stable individual behavioural style, correlated with hormonal differences (Pfeffer et al. 2002).

For the moment, the only cognitive ability that seems to show negative correlations with the others is the spatial memory used by food storing Corvidae and Paridae (Lefebvre and Bolhuis 2003). It is on two of these species of foodstoring corvids that Templeton et al. (1999) found the only evidence for a negative relationship between social and individual learning. In Templeton et al.'s study, the more social pinyon jay showed faster social learning than the more solitary Clark's nutcracker, with species differences in individual learning going in the opposite direction. Taken together, however, our results and the vast majority of studies available suggest no trade-off between social learning and individual routes to innovation and learning.

If this is generally the case, new feeding techniques would spread rapidly through populations, as individuals that generate innovations at a high rate would also have access to the innovations of others through fast social learning. If acquiring the new techniques had a strong effect on survival, there would be a much stronger fitness differential within the population than under zero or negative correlations between innovation and social learning. This is because individuals that do poorly on innovation tend to also do poorly on social learning and thus have little or no access to the new technique through either process. This is in sharp contrast to the individuals that both learn quickly from others and innovate often. An obvious next step would be to simulate the effects of these fitness differentials and cultural transmission rates on behavioural drive.

Our field experiment shows that the innovation we studied in captivity can spread in a wild population, in line with the results obtained by Webster and Lefebvre (2001). However, the success rate of pigeons (35 of 42 individuals in captivity and eight of 12 flocks in the field) was much higher than that obtained by even the most innovative species tested by Webster and Lefebvre, the Carib grackle Quiscalus lugubris (six of 15 in captivity and two in the field). Moreover, when we look at results from the two species that are taxonomically closest to our pigeons, the zenaida dove Zenaida aurita and common ground dove Columbina passerina, success rates are even lower; only one of 30 individuals (3%) solved the problem in captivity and no dove opened the box in the field (Webster and Lefebvre 2001). In a study of individual learning and neophobia, Seferta et al. (2001) also noticed a marked difference in performance between feral pigeons and Zenaida aurita. When data on reversal learning in eight avian species (taken from Gossette 1968) were examined, pigeons again are outliers and perform much better than expected from their innovation rate and brain size (Timmermans et al. 2000; Lefebvre and Bolhuis 2003). This apparent superiority of pigeons is probably a result of artificial selection. All pigeons in the New World descend from captive individuals and are thus presumably bred for tolerance of captive conditions and human proximity (Johnston and Janiga 1995). It is not a coincidence that feral pigeons are often the species chosen in captive experiments; they tolerate experimental conditions much better than many other species, and consequently perform well on a variety of tasks. It would be important to conduct a similar study on a species that has not gone through artificial selection to make sure the positive correlation between innovation and social learning found here is a general one.

Our results seem to be at variance with earlier studies on flexible individual roles in pigeon foraging flocks. Both theoretical (Giraldeau 1984) and empirical work (Giraldeau and Lefebvre 1986, 1987) suggest that pigeons in groups have flexible producing specialisations that change from one feeding situation to the next, yielding a skill pool when each bird can scrounge the specialisations of others on tasks where it has not learned to produce. In both the theoretical and empirical work, producing specialisations are uncorrelated across individual pigeons over different tasks. In the skill pool hypothesis (Giraldeau 1984), it is the chance effect of

encounters with food rewards that determines who learns in any given situation, added to the incompatibility between producing and scrounging and the inhibitory effect of group scrounging on learning (Lefebvre and Helder 1997). Our finding that performances across learning situations are positively correlated thus differs from the zero correlations envisioned by the skill pool. More work is needed to reconcile these differences, but one intriguing possibility is that the frequency-dependent payoffs that act in a group situation override the individual differences that show up in single cage experiments like ours. Such a finding would support the point made by Giraldeau and Caraco (2000) for learning and Morand-Ferron et al. (2004) for innovations, that frequency-dependent payoffs can be more important than individual abilities in determining whether or not a behaviour will occur in a given social foraging situation.

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References

- Both C, Dingmanse NJ, Drent PJ, Tinbergen JM (2005) Pairs of extreme avian personalities have the highest reproductive success. J Anim Ecol 74:667–674
- Carere C, Drent PJ, Privitera L, Koolhaas P, Groothuis TGG (2005) Personalities in great tits, *Parus major*, stability and consistency. Anim Behav 70:795–805
- Dingmanse NJ, Réale D (2005) Natural selection and avian personality. Behaviour 142:1159–1184
- Fisher J, Hinde RA (1949) The opening of milk bottles by birds. Br Birds 42:347–357
- Fragaszy DM, Perry S (2003) Towards a biology of traditions. In: Fragaszy DM, Perry S (eds) The biology of traditions: models and evidence. Cambridge University Press, Cambridge, UK, pp 1–32
- Galef BG Jr (1996) Social enhancement of food preferences in Norway rats: a brief review. In: Heyes CM, Galef BG Jr (eds) Social learning: the roots of culture. Academic, San Diego, CA, pp 49–64
- Giraldeau LA (1984) Group foraging: the skill pool effect and frequency-dependent learning. Am Nat 124:72–79
- Giraldeau LA, Caraco T (2000) Social foraging theory. Princeton University Press, Princeton, NJ
- Giraldeau LA, Lefebvre L (1986) Exchangeable producer and scrounger roles in a captive flock of feral pigeons: a case for the skill pool effect. Anim Behav 34:797–803
- Giraldeau LA, Lefebvre L (1987) Scrounging prevents cultural transmission of food-finding behaviour in pigeons. Anim Behav 35:387–394
- Giraldeau LA, Templeton JJ (1991) Food scrounging and diffusion of foraging skills in pigeons, *Columbia livia*: the importance of tutor and observer rewards. Ethology 89:63–72
- Gossette RL (1968) Examination of retention decrement explanation of comparative successive discrimination reversal learning by birds and mammals. Percept Mot Skills 27:1147–1152

- Greenberg R (1983) The role of neophobia in determining the degree of foraging specialization in some migrant warblers. Am Nat 122:444–453
- Greenberg R (1984) Differences in feeding neophobia in the tropical migrant wood warblers *Dendroica castanea* and *D. pensylvanica*. J Comp Psychol 98:131–136
- Greenberg R (1990b) Feeding neophobia and ecological plasticity: a test of the hypothesis with captive sparrows. Anim Behav 39:375–379
- Heyes CM, Galef BG Jr (1996) Social learning in animals: the roots of culture. Academic Press, New York
- Johnston RF, Janiga M (1995) Feral pigeons. Oxford University Press, New York
- Kummer H, Goodall J (1985) Conditions of innovative behaviour in primates. Phil Trans R Soc Lond B 308:203–214
- Lefebvre L (1986) Cultural diffusion of a novel food-finding behaviour in urban pigeons: an experimental field test. Ethology 71:295–304
- Lefebvre L, Bolhuis JJ (2003) Positive and negative correlates of feeding innovations in birds: evidence for limited modularity. In: Reader SM, Laland KN (eds) Animal innovation. Oxford University Press, Oxford, pp 40–61
- Lefebvre L, Bouchard J (2003) Social learning about food in birds. In: Fragaszy DM, Perry S (eds) The biology of traditions: models and evidence. Cambridge University Press, Cambridge, UK, pp 94–126
- Lefebvre L, Giraldeau LA (1996) Is social learning an adaptive specialization? In: Heyes CM, Galef BG Jr (eds) Social learning in animals: the roots of culture. Academic, New York, pp 107–128
- Lefebvre L, Helder R (1997) Scrounger numbers and the inhibition of social learning in pigeons. Behav Proc 40:201–207
- Lefebvre L, Palameta B, Hatch KK (1996). Is group-living associated with social learning? A comparative test of a gregarious and a territorial Columbid. Behaviour 133:241–261
- Lefebvre L, Whittle P, Lascaris E, Finkelstein A (1997) Feeding innovations and forebrain size in birds. Anim Behav 53:549–560
- Lefebvre L, Reader SM, Sol D (2004) Brain, innovation and evolution in birds and primates. Brain Behav Evol 63:233–246
- Martinez del Rio C (1993) Do British tits drink milk or just skim the cream? Brit Birds 86:321–322
- Morand-Ferron J, Lefebvre L, Reader SM, Sol D, Elvin S (2004) Dunking behaviour in Carib grackles. Anim Behav 68:1267–1274
- Nicolakakis N, Sol D, Lefebvre L (2003) Behavioural flexibility predicts species richness in birds, but not extinction risk. Anim Behav 65:445–452
- Pfeffer K, Fritz J, Kotrschal K (2002) Hormonal correlates of being an innovative greylag goose, Anser anser. Anim Behav 63:687–695
- Reader SM, Laland KN (2001) Primate innovation: sex, age and social rank differences. Int J Primatol 22:787–805
- Reader SM, Laland KN (2002) Social intelligence, innovation and enhanced brain size in primates. Proc Natl Acad Sci USA 99:4436– 4441
- Reader SM, Laland KN (2003) Animal innovation. Oxford University Press, Oxford
- Sasvári L (1985a) Keypeck conditioning with reinforcement in two different locations in thrush, tit and sparrow species. Behav Proc 11:245–252
- Sasvári L (1985b) Different observational learning capacity in juvenile and adult individuals of congeneric bird species. Z Tierpsych 69:293–304
- Seferta A, Guay PJ, Marzinotto E, Lefebvre L (2001) Learning differences between feral pigeons and zenaida doves: the role of neophobia and human proximity. Ethology 107:281–293
- Sherry DF, Schacter DL (1987) The evolution of multiple memory systems. Psychol Rev 94:439–454
- Shettleworth SJ (1998) Cognition, evolution and behaviour. Oxford University Press, Oxford

- Sih A, Bel AM, Chadwick-Johnson J, Ziemba RE (2004) Behavioral syndromes: an integrative review. Q Rev Biol 79:241–277
- Sol D, Stirling DG, Lefebvre L (2005) Behavioral drive or behavioral inhibition in evolution: subspecific diversification in Holarctic passerines. Evolution 59:2669–2677
- Templeton JJ, Kamil AC, Balda RP (1999) Sociality and social learning in two species of corvids, the pinyon jay (*Gym-norhinus cyanocephalus*) and the Clark's nutcracker (*Nucifraga columbiana*). J Comp Psych 113:450–455
- Timmermans S, Lefebvre L, Boire D, Basu P (2000) Relative size of the hyperstriatum ventrale is the best predictor of feeding innovation rate in birds. Brain Behav Evol 56:196–203
- Webster SJ, Fiorito G (2001) Socially guided behaviour in non-insect vertebrates. Anim Cogn 4:69–79
- Webster SJ, Lefebvre L (2001) Problem solving and neophobia in a columbiform-passeriform assemblage in Barbados. Anim Behav 62:23–32
- Whittle PJ (1996) The relationship between scramble competition and social learning: a novel approach to testing adaptive specialisation theory. M Sc Thesis, McGill University, Montréal, Canada
- Wilson AC (1985) The molecular basis of evolution. Sci Am 253:148– 157
- Wyles JS, Kunkel JG, Wilson AC (1983) Birds, behavior and anatomical evolution. Proc Natl Acad Sci USA 80:4394–4397