Individuality in Problem Solving: String Pulling in Two *Carduelis* Species (Aves: Passeriformes)

Uta Seibt & Wolfgang Wickler

Max-Planck-Institut für Verhaltensphysiologie Seewiesen, Starnberg, Germany

Correspondence
Prof Dr Wolfgang Wickler, Max-Planck-Institut für Verhaltensphysiologie Seewiesen, D-82319 Starnberg, Germany.
E-mail: wickler@orn.mpg.de

Received: March 9, 2005
Initial acceptance: July 11, 2005
Final acceptance: September 9, 2005
(M. Taborsky)

doi: 10.1111/j.1439-0310.2005.01172.x

Abstract

The research reported here was designed to study the individual peculiarities of birds in solving a problem. Goldfinches *Carduelis carduelis* and siskins *C. spinus* were tested with the string-pulling task: sitting on a perch from which a small food container is suspended by a string the test bird had to lift the container, using the bill to pull the string stepwise up and a foot to hold it, and repeat that until they could reach the food. Fifty-two goldfinches and 29 siskins raised under controlled conditions were tested individually. Three groups became apparent: 'inventors' (23% of goldfinches; 62% of siskins) solved the problem by themselves; 'imitators' (25% of goldfinches; 10% of siskins) succeeded after seeing a performing conspecific; 'duffers' (52% of goldfinches, 28% of siskins) did not succeed either way. The species – but not the sexes – differed significantly in string-pulling ability. The results of our experiments indicate that string pulling is an acquired combination of innate behaviour elements. An individual's string-pulling competence may depend on prior experience of handling branchlets, on trial-and-error learning and on social learning (emulation). However, some individuals succeeded without these facilitating factors, while others did not succeed at all despite all of them present. Although functionally and motivationally related to feeding, the learned string pulling is often shown as a playful activity without an obvious reward.

Introduction

A famous example of problem solving in birds is the string-pulling tactic. In an experimental setup a bird can obtain food by lifting a small food container suspended from a perch by a string. This behaviour is known as a popular entertainment since ancient times, in particular from goldfinches. It was mentioned by Plinius (1554), by Albertus Magnus in 1250, by the Italian historian Bartolomeo de Sacchi (1421–1481) as well as by Gesner (1669). In modern times string pulling has caught the scientists' interest as being a special problem-solving ability. Various reports dealt with casual and systematic observations of string pulling in different birds: in corvids (Hertz 1926; Heinrich 1995, 2000), a garden warbler (Teyrovský 1930), in siskins (Thienemann 1933), larger parrots (Fischel 1936) and in parids and finches (Herter 1940; Vince 1956, 1958, 1961).

Erhardt (1933) thought that string pulling derives from normal instinctive feeding behaviour and does not require intelligence. Likewise, Vince (1958, 1961) and Altevogt (1954) saw no need to apply terms like 'insight' and 'understanding' to this behaviour. Bierens de Haan (1933) suggested that string-pulling behaviour is not purely genetically determined but will need some intelligence, i.e. a capacity to have the behaviour influenced by individual experiences. Heinrich (1995, 2000) concluded from his experimental study that insight into the situation plays a role, and Thorpe (1956) postulated that in string pulling a combination of insight learning, tool using and innate behaviour patterns is involved.

Species can be expected to differ in their predisposition to solve manipulative tasks if they are adapted to different habitats (Dukas 1998), as is clearly the case for finches, tits, ravens or parrots used in string-pulling studies by earlier authors. As we were interested mainly in causes of individual variation of the propensity and capability to perform string pulling we chose to test two closely related species that co-occur in the same habitat, share their main foraging techniques and should therefore be expected to show similar manipulative capabilities and string-pulling behaviour. We selected species the behaviour of which is well known from the field, and which readily breed in captivity and which can be reared under controlled conditions. Seed eaters can be more easily kept and handled in captivity than insect eaters. So we selected two species of the same genus, goldfinch *Carduelis carduelis* and siskin *C. spinus*, which are adapted to a similar habitat. Both species are dexterous climbers who like to pick buds from branchlets of trees like *Alnus* as well as small seeds from exposed positions on Compositae and Gramineae. The birds may even pull several grass stems together and grasp them with their feet (Perrins 1994).

While sex differences may be genetically determined, different epigenetic influences should result in inter-individual differences in performance. We confronted birds that were raised under similar, controlled conditions with the string-pulling task which can be expected to involve both genetic and epigenetic determinants. Individuals may then differ in the performance according to their individual prior experience. We analysed how many individuals solved the task and how differently individuals attacked the problem, and we tested for species- and sex specificities in performing the task. Finally, we tested for the importance of two possible kinds of learning: individual early habitat experience and social learning.

Methods

Subjects and Housing

For our experiments we used 52 goldfinches and 29 siskins. All of them had been reared in aviaries by their parents for up to 6–8 wk of age. To exclude an influence of early experience with branchelets and any other natural material that could be pulled in, we raised from hatching 12 goldfinches and two siskins in conditions without any objects that could be used to practice string-pulling movements. All birds were experimentally tested as subadults with up to 5 mo of age (for goldfinches minimum age 6 wk, $\bar{x} = 13.7$ wk; for siskins minimum age 8 wk, $\bar{x} = 13.6$ wk). At that age they had already the adult body weight of about 15 g.

From 2 mo of age onwards the string-pulling naive birds were kept singly for the whole test period in $57 \times 58 \times 29$ cm (L × H × W) sized cages. They were visually isolated from each other and rapidly habituated to their new home. To avoid stressful handling all individuals were tested in their holding cages. The cages contained three sitting perches, one in the upper half and two below (Fig. 1). The birds had access to food (small husked grain for seed eaters) and water in commercial feeders ad libitum, except for the 1 h test periods.

Test Situation

For the tests the uppermost sitting perch was exchanged for a similar one with a thimble suspended by a thin (0.3 mm diameter) red string, 7 cm long. The stringed thimble was introduced into the cage just once per day and for the observation period only. The thimble itself was out of reach for the bird from either perch as well as from the sides of the cage. The empty thimble (1.5 cm diameter, 2.5 cm deep) weighed 3 g; it was filled with 2 g of food, identical to the food in the commercial feeder.

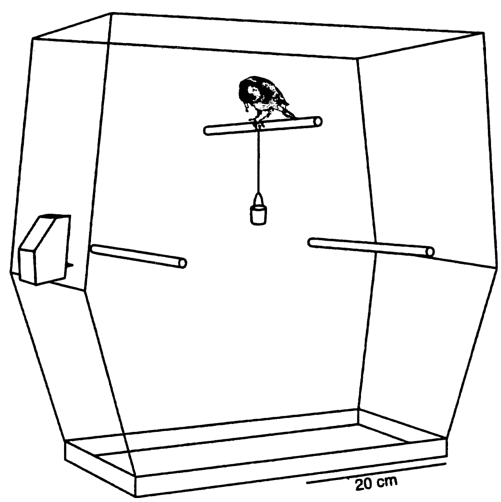

Fig. 1: Standard cage with commercial feeder and sitting perches; in the test situation the upper perch holds the thimble suspended by a 7-cm string, out of reach for the bird from either perch as well as from the sides of the cage

To obtain food from the thimble the bird had to perch above the stringed thimble, reach down, pull up a loop of string with the bill, set the looped-up string onto the perch, step onto the string, release the string from the bill while holding the loop with the foot, and then reach down again to repeat the whole performance (Fig. 2). The individuals used one foot as the supporting leg, bent the body to its side and raised the other foot to grasp the string. Complete string pulling needed 2–3 successive pullings with the bill and holding the pulled-up loop with a foot; only then the bird could reach the food. From 4645 filmed string-pulling and holding acts (feeding included) performed by seven goldfinches between 62% and 87% of the acts of each bird lasted about 1 min, the other acts lasted up to 10 min.

Testing Protocol

The birds did not show string pulling continuously throughout the test sessions but were also preening, sitting as in sleep, looking around or moving around, often in bouts of up to 10 min. Therefore, the test sessions lasted for 1 h to provide enough time to observe string pulling.

Individual birds were exposed to the test situation in 10 one-hour solo sessions, one session per day, and with different intervals between the test days. We tested the birds at different times of day with only the test bird(s) and one observer in the room. Individuals that did not achieve perfect string pulling during the solo sessions were exposed to a string-pulling conspecific in a neighbouring cage for several subsequent model sessions (up to 24), with both cages put 5 cm apart from each other.

The tests were run with goldfinches from November 1999 to August 2000 and with siskins from July 2001 to February 2002. The birds were observed between 9 and 12 h and 13–15 h; later in the day they were less active, in particular during winter. During the test sessions the occurrence of each categorized behaviour was noted (yes or no) once per minute on prepared test-sheets. One-minute intervals were indicated acoustically. The birds' performances in the tests were recorded by three different persons. Two of them, who did the majority of recordings, were not informed about the underlying hypotheses. In addition to the direct observations we video-recorded sequences of 3–10 min length (haphazardly chosen) of about 10% of the observed performances (using a Sony Digital Video Camera DVR TRV9E; Sony Corporation, Tokyo, Japan; 25 frames per second). These recordings were analysed by all three observers to test for observer bias. However, the behaviour categories turned out to be defined so strictly that observers' scores did not differ. For species comparisons we used 867 sessions with goldfinches and 139 sessions with siskins (shown in Fig. 3).

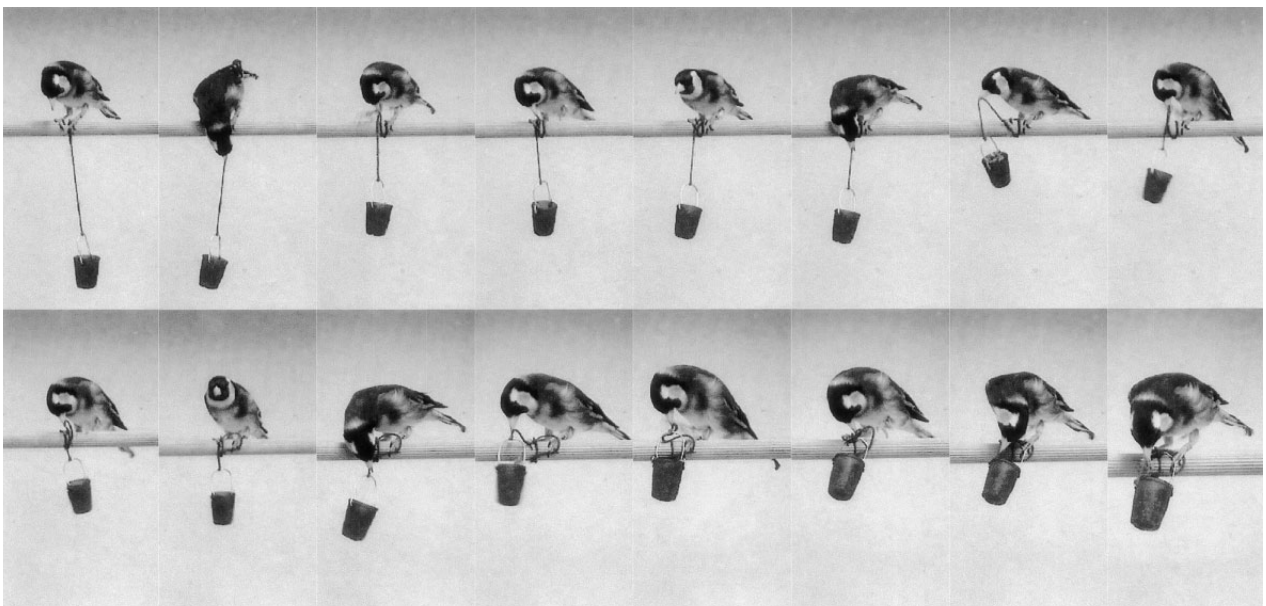

Fig. 2: A goldfinch uses its bill to pull the string stepwise up in coordination with a foot to hold it, and picks grains from the thimble (composed from a video, illustrating typical transitions but not real durations of actions)

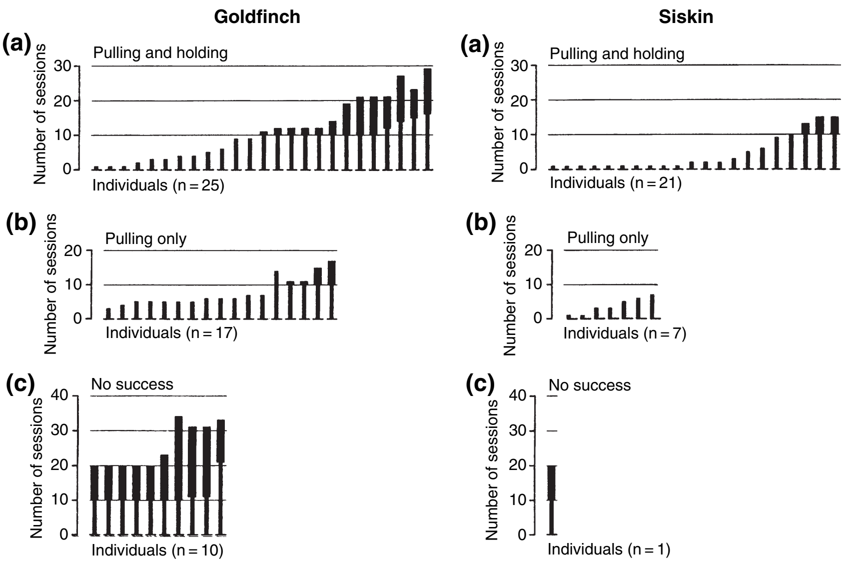

Fig. 3: Number of test sessions required by individual goldfinches and siskins until first successful performance of pulling and holding (a), or pulling only (b), and the number of sessions without success (c). Narrow bars: sessions without model bird; broad bars: sessions with model bird. The upper ends of columns in panels a and b indicate the birds' first performance, and in panel c they indicate termination of the (unsuccessful) test series.

Further sessions were added to test for consistency of the string-pulling behaviour.

The following behaviours were recorded: focussing the thimble, billing the string, pull the string with the bill and drop it back (pulling only), step onto the pulled-up string (pulling and holding), eating from thimble.

We counted the number of test hours per individual up to the first occurrence of 'pulling and holding', or – if this did not occur – up to 'pulling only'. The birds that eventually showed pulling and holding during the solo sessions were categorized as 'inventors' (narrow bars in Fig. 3a). Birds which finally showed pulling and holding in view of a demonstrating conspecific after they had been tested alone in at least 10 sessions were named 'imitators' (broad upper bars in Fig. 3a). In the goldfinch analysis there are four individuals included that were initially given more than 10 solo sessions and only then were confronted with the performing model bird. Thereafter we set the limit to 10 solo sessions for all subsequent birds. Individuals which had not shown pulling and holding after 10 sessions alone plus at least 10 (up to 24) sessions with a demonstrator were classified as 'duffers' (all bars in Fig. 3b, c). For statistical procedures we follow Sokal & Rohlf (1981).

Results

How Many Individuals Solved the Problem?

Figure 3 shows the number of sessions after which each individual first performed either string pulling and holding (panel a) or pulling only (panel b), both alone and with a model. Fig. 3b, c indicates for the duffer individuals of both species the number of sessions, alone and with model, that each individual was exposed to without ever showing string pulling and holding.

Obviously within both species individuals behaved very differently (Fig. 3). Some birds had no difficulty in solving the task immediately or within a few sessions with only little preliminary mandibulating the string. Others seemed interested in the situation but incapable to lift the thimble.

How Did Individuals Approach the Problem?

All individuals of both species which succeeded in string pulling also tried various other ways to take food from the thimble. Several individuals of both species hovered in flight near the thimble. They never succeeded in taking food, but still tried to reach food this way when they were already able to eat via string pulling and holding. A few goldfinches and siskins stretched from the cage fence towards the thimble but without successfully touching it. Two siskins and one goldfinch reached the thimble while hanging down from the perch head down like bats. Several siskins climbed down the string and ate from the thimble. Three other siskins shed some food from the thimble by heavily shaking the string and pecked the grain from the floor. (Goldfinches never moved to the cage floor.) Eight goldfinches and seven siskins invented a special method to flick the string around the perch, thus lifting the thimble indirectly. Some individuals used several of these techniques.

All successful string-pulling individuals (25 goldfinches, 21 siskins) varied their pulling and holding performance. They either pulled successive loops of the string on the spot, or they sidled to the left or right, stretching the string along the perch. They held the string sometimes with the right, at other times with the left foot, or used both feet. Two goldfinches and eight siskins showed handedness, consistently using the same right or left foot.

Duffers might have failed either because they were too unskilful or just uninterested. A frequent behaviour of all birds was to nibble and tug at the string-noose which encircled the perch, and to mandibulate the knot or the string. We called this behaviour inquisitive probing (IP). If this indicated a general interest of a bird in the situation, one would expect differences in the occurrence of IP between 13 imitators (final individuals in Fig. 3a) and 10 duffers (all individuals in Fig. 3c) during their 10 solo sessions where not even pulling only occurred. We counted for these 23 goldfinches the number of sessions in which IP behaviours occurred in each bird. The data showed no difference between the two groups (13 imitator birds: $\tilde{x} = 2.0$, first quartile 1.0, third quartile 8.0; 10 no-success birds: $\tilde{x} = 3.5$, first quartile 2.0, third quartile 9.0; U-test: $p = 0.4$; $U = 53$, $N = 13 + 10$). However, IP behaviour continued to be shown by several individuals which performed perfect string pulling. It did continue for minutes on end, independent from string pulling and not immediately prior to it, therefore it is apparently not an attempt to pull the string.

Species and Sex Differences in String-Pulling Performance

Species differences

We compared the numbers of 'inventors' plus 'imitators' (successful individuals) with the numbers of duffers in both species. Among 52 goldfinches we had 25 successful (48%) and 27 duffer (52%) individuals, among 29 siskins 21 successful (72%) and eight duffer (28%) individuals (Fig. 3). Siskins performed significantly better than goldfinches (G-test with Williams correction: $G = 4.523$; $df = 1$; $p = 0.033$). Thirteen of 25 successful goldfinch individuals and three of 21 successful siskins were imitators. Learning from a model seems less important in siskins than in goldfinches (G-test with Williams correction: $G = 7.324$; $df = 1$; $p = 0.007$). Among the 40 goldfinches that grew up with branchlets (comparable with natural conditions) 11 were 'inventors' and 12 were 'imitators'. Among 27 siskins that grew up with branchlets we found 16 'inventors' and three 'imitators' (see Fig. 3). This difference between the species is significant (two-tailed Fisher's exact test; $p = 0.023$).

Sex differences

We compared successful (inventors and imitators) and duffer individuals according to their sex (for birds whose sex was known; Table 1). We found no significant difference (two-tailed Fisher's exact tests) between the sexes for 36 goldfinches ($p = 0.086$), and for 29 siskins ($p = 0.68$).

Is Social Learning Involved?

Most individuals of both species that had not shown string pulling and holding after 10 solo sessions were exposed to a perfectly performing conspecific (Fig. 3a, broad upper bars). Using the goldfinch data we tested (1) whether the observer birds paid attention to the model's activities, and (2) whether imitators copied the model bird's version of string-pulling behaviour.

Testing for attention

Method. Cages of the two birds were positioned about 5 cm apart. We counted as 'inspection' when an observer bird directed its gaze (i.e. pointed with the bill) towards the model neighbour, sometimes with turning its head along the longitudinal axis, or even climbed on to the cage fence near the neighbour and inserted the bill between the cage rods.

As most string-pulling acts lasted for about 1 min we recorded the birds' activities within 1-min time windows per 1-h session. We counted the number of minutes (A) when pupil's inspection and model's

Table 1: String-pulling performance in females and males of 36 goldfinches and 29 siskins with known sex

Test birds	Inventors and imitators	Duffers
Goldfinch		
Males	14	8
Females	4	10
Siskin		
Males	8	4
Females	13	4

string pulling coincided, (B) when the model bird pulled the string without the pupil bird inspecting; (C) when the pupil bird inspected while the model bird did not pull the string but performed some other activity. We calculated the number of pupil bird's inspection and model bird string pulling co-occurring by chance within the same minute and compared it with the observed number of co-occurrences. The expected chance coincidence of the model's string pulling and the pupil's observing within the same minute and within a period of 60 min (E) was calculated as:

$$E = \frac{(A + B)(A + C)}{60}.$$

The difference A − E then shows whether the observer bird inspected more (A > E) or less (A < E) often than expected by chance in the same minutes in which the model performed string pulling.

We recorded the behaviour of 10 imitators and 10 birds without success in visual contact with the same reliably string-pulling model individual (male 478).

Results. The coincidence of the model's string pulling and the observer test bird's observing was in all cases higher than expected by chance (Binomial test; $p = 0.002$; Table 2). This supposed interest of the observer birds in the model bird's string pulling did not differ significantly between imitators and non-imitators as shown by the comparison between differences (A − E) in Table 2 (U-test: N = 10 + 10, U = 42.5; $p > 0.5$).

Table 2: Distribution of inspection behaviour of 10 goldfinch observer birds when a model bird was pulling a string (see text for explanation of the test logic)

Test bird no.	A	B	C	E	A–E
Imitators					
090	7	10	10	4.8	2.2
098	7	0	10	2.0	5.0
104	5	3	5	1.3	3.7
021	1	12	2	0.7	0.3
018	3	19	3	2.2	0.8
108	2	4	0	0.2	1.8
107	11	5	3	3.7	7.3
078	6	16	0	2.2	3.8
035	10	5	3	3.3	6.7
046	10	3	6	3.5	6.5
Non-imitators					
099	16	6	16	11.7	4.3
117	21	2	16	14.2	6.8
001	3	11	2	1.2	1.8
003	1	5	0	0.1	0.9
005	7	3	1	1.3	5.7
070	9	11	1	3.3	5.7
024	6	15	2	2.8	3.2
042	8	11	3	3.5	4.5
087	10	18	5	7.0	3.0
050	14	9	1	5.8	8.2

A: observer bird's inspection and model's string pulling coinciding within the same minute; B: model bird's string pulling without observer bird inspecting within the same minute; C: observer bird inspected while model bird did not string pull within the same minute; E: expected chance coincidence of model's string pulling and observer's observing within the same minute; A–E: difference indicating observer's special interest in model's string pulling.

Testing for imitation

Method. Model and observer birds in separate cages were in close contact as described. From our behavioural records of sessions containing an imitator's first successful performance we noted both birds' string-pulling behaviour. Model birds showed four behaviour categories that were sufficiently distinct: (1a) pulling the string while sitting on the spot or (1b) stretching the string along the perch (to the left or right); and (2a) holding the string with one foot (right or left) or (2b) with both feet.

Results. Records from 13 goldfinch imitators' first performance sessions were available, which we used to test whether or not they exactly copied the model bird's performance. Nine model birds exhibited all four behaviours, and seven of their corresponding observer birds did so as well. Two imitators showed fewer variants than the model had shown. Three imitators pulled the string on the spot despite the fact that the model bird did not do so, and one imitator stretched the string to the left without having seen this from the model. We conclude that a close correspondence between models' and imitators' string-pulling behaviour was not apparent, but the data set did not allow for a conclusive test.

Eight goldfinches and seven siskins performed a special method to flick the string around the perch, thus lifting the thimble. Six goldfinches and all siskins invented this method by themselves after they had already shown string pulling and holding. Two observer goldfinches started string flicking after having seen a conspecific doing it (one 38 min, the other 11 d after). All these individuals used string flicking rarely and not as the preferred technique.

The Influence of Food Reward on String Pulling

In a pilot experiment we tested whether food in the thimble had an effect on string pulling. Two reliably string-pulling goldfinches (males 15 and 478) were observed in the same way as throughout the study. We offered in random sequence the thimble full or empty (ten 1-h sessions each). Male 15 showed string pulling and holding 19 times with the full thimble and once with the empty thimble; the respective numbers for male 478 were 50 and nine times. Both males lifted the full thimble significantly more often than the empty one (Fisher's exact test; $p < 0.001$ for male 15, $p = 0.026$ for male 478). However, male 15 did not eat from the full thimble in 26% of a total of 78 string-pulling cases and male 478 in 23% of its 116 string-pulling cases.

Does Early Experience Influence an Individual's String-Pulling Behaviour?

Most of our study birds had grown up in aviaries supplied with branches and branchlets that provided training opportunities. Pulling in thin branches or grass stems is part of the birds' normal feeding technique. Having practiced such feeding behaviour may have an influence on the ability to later solve the string-pulling task.

To test the role of pulling in branches or stems during ontogeny we raised 12 goldfinches and two siskins under controlled conditions without any objects that they could have used to practice string-pulling movements. For the goldfinches we compared their performance in our standard tests with the performance of 40 goldfinches raised with ample opportunities to handle branches.

The group reared without branches contained two string-pulling and holding individuals and 10 duffers. The group reared with branches contained 23 string-pulling and holding individuals and 17 duffers. This suggests that early opportunity to handle twigs has a positive effect on later string-pulling behaviour (G-test with Williams correction: $G = 6.464$, $df = 1$; $p = 0.012$).

However, 17 of 40 goldfinches and eight of 27 siskins raised with ample opportunities to handle branches did never show string pulling and holding. However, among 12 goldfinches reared without branches we found one inventor and 1 imitator; also, both siskins reared without branches were inventors. These results show that despite an apparent facilitation effect, practicing experience during ontogeny is not necessary for a successful string-pulling performance.

Discussion

Basic Elements of String-Pulling Behaviour

The two main components of string-pulling behaviour are pulling the string with the bill, and afterwards holding the string with a foot. Mandibulating or pulling any object with the bill is a common behaviour of all birds and may be seen as a multifunctional behavioural tool (sensu Lorenz 1939), which is used in various contexts. In our tests, pulling the string (pulling only) with the bill was shown by many individuals which never succeeded in complete pulling and holding (Fig. 3b). On the contrary, all individuals which achieved complete string pulling and holding nevertheless continued to perform pulling only (Seibt 2002). Although part of the required skill, this behaviour can be performed for its own sake and does not always represent an abortive string-pulling and holding action.

Holding food with the feet is shown by birds of different taxonomic families (Millikan & Bowman 1967; Clark 1973) and in different unrelated passerines; it seems to be basically inherited but can be further perfected through learning (Vince 1961; Clark 1973). A genetic inheritance of holding in *Carduelis* is indicated by Hinde's (1956) hybridization studies on cardueline finches: while crosses of *C. carduelis* with canaries and greenfinches often held food with their feet, hybrids between canary and greenfinch did not.

In our experiments the birds had to precisely coordinate the two behavioural elements, pull in with the bill and hold with a foot. The fact that 33% of all 52 goldfinches and 24% of all 29 siskins showed pulling only but did not use the foot for holding indicates that stepping on the pulled-up string is the most critical part of the performance, as suggested by Heinrich (1995) for ravens. From our test birds that were raised with branches, 11 of 40 goldfinches (27.5%) and 16 of 27 siskins (59.3%) solved the string-pulling problem within one to ten 1-h sessions (Fig. 3a, narrow bars). Also, most individuals went on to vary details of this coordination, suggesting that the performance remains variable.

Learning by practicing may have played a role for those individuals which performed pulling and holding during the first 10 sessions (Fig. 3a, narrow bars). It is not necessary, however, to assume insight into the problem for the individuals which performed perfectly already during the first session (three goldfinches and 10 siskins). It suffices that in an individual, which by random chance steps onto the pulled-up string, 'insight may have followed so that the random discovery could be instantly exploited' (Heinrich 1995). This may not be different from operant conditioning and may happen at any time in the series of test sessions, early in some individuals, later in others.

Social Learning

Some kind of social learning was suggested for 13 goldfinches and three siskins which had not solved the problem within the solo sessions but were successful after repeatedly seeing a performing conspecific (Fig. 3a, broad bars). We classified them as imitators, although we cannot exclude the possibility that they might have eventually solved the problem by themselves at some later time. To support our suggestion that social learning may have been relevant, we quantified 20 supposed learners' interest in one and the same model bird's string-pulling behaviour. Not just the 10 imitators but also 10 individuals which remained incompetent for string pulling revealed a significant interest in the string-pulling activity of the neighbouring conspecific individual (see Table 2). Such specific attention is seen as a precondition of social learning. However, this attention did not differ significantly between imitators and birds which remained unsuccessful.

Typically, the interest of the imitator in the model's activities is expressed as it sits next to the cage wall watching the model, then sidles back to peck at its own string, again positions itself close to the model, goes back and pulls at its string, all this a bit hastily and with slightly fluffed feathers. This may go on back and forth for some time until finally the imitator string pulls for the first time. To us the imitator seemed fairly agitated. The model in contrast, though active all the time, appeared less tense and less interested in the activities of its neighbour.

The string-flicking method was clearly invented by six goldfinches; two more goldfinches which started the string-flicking method after having had the chance to see it in another bird (11 d earlier in one case) may have invented the method by themselves too, rather than having copied it from the model.

For nine goldfinch imitators [see chapter 4 (2) 'Testing for imitation'] which performed all, or some of, the string-pulling behaviour variants that were also shown by the model birds we cannot decide whether they just tried out these variants or truly imitated them. Those four imitators which performed a variant that had not been shown by the model seem to have caught the goal and duplicated the result of the model's behaviour, though not its method. This type of social learning has been termed 'goal emulation' by Wood (1989).

Species-Specific Performance of String Pulling

Goldfinches and siskins are genetically very closely related. A highly developed foot-bill coordination to pull in branchlets with the bill and clamp them under a foot in the context of foraging has been reported for both species from the field (Perrins 1994), although it will be difficult to test under field conditions how many individuals of a species actually use this behaviour. When testing for the string-pulling performance, which resembles one of their foraging techniques, these birds should be expected to show interindividual differences as documented for string pulling of several other unrelated bird species (Herter 1940; Vince 1956; Heinrich 1995, 2000). But we also found clear species-specific differences. About 48% of goldfinches grown up with branchlets and 72% of similarly raised siskins showed string pulling successfully. Hence comparing the performance of both species in our tests, siskins were more successful in solving the string-pulling problem than goldfinches, while a supposed social learning effect was significantly less important in siskins. The sexes did not differ significantly in their string-pulling performance in either species, despite a tendency that male goldfinches were more successful than females.

Individuality

Clearly individuals of both species coped differently with the situation. However we have no independent behavioural data to show whether or not individuals follow coping styles as defined for instance by Wechsler (1995) or Koolhaas et al. (1999). Individual-specific behaviour may be influenced by an individual's history. We found two external factors that can influence an individual's string-pulling performance: in goldfinches it seems to be enhanced by the opportunity to observe string-pulling conspecifics, and it is facilitated clearly by early experience in handling branches and plant stems. Handling branches has the bill–foot coordination in common with string pulling. Nevertheless, to eventually perform string pulling early twig handling proved to be only partially important, as it was not necessary for some individuals, while it did not appear to help others.

One goldfinch and two siskins solved the string-pulling task without prior handling branches and without ever seeing a model bird performing this behaviour. Others, with both prior manipulation experience and a social tutor, did not succeed at all.

The development of a complex feeding technique has been studied also by Tebbich et al. (2001) in the woodpecker finch *Cactospiza pallida*. The bird uses twigs or cactus spines as tools to lever arthropods out of tree holes and crevices. This behaviour has an innate component that causes all young individuals to playfully mandibulate twig-like objects. In addition early handling of sticks is necessary to learn by trial and error how to insert twigs into crevices to obtain prey as a reward and thus to develop the full tool-use as a foraging technique. In our birds, the motivation to pull in and hold branchlets in order to feed on terminal buds during winter may have an innate basis. The opportunity to manipulate branchlets early in ontogeny facilitates later learning how to pull strings. At least the inventors could have succeeded by a stepwise trial-and-error learning, if any activity that put the thimble in motion without lifting it fully was already rewarding. And food as a reward (see 'Motivational aspects', below) seems important, too, as it is in the cactus finch, pointing towards a potential role of operant conditioning.

Motivational Aspects

String pulling seems functionally and motivationally related to handling plant stems and branchlets while feeding. In his study on common ravens, *Corvus corone*, Heinrich (1995) always had food attached to the strings; string pulling clearly was food directed. However, in his study on tits, *Parus major*, *P. caeruleus* and *P. ater*, Altevogt (1954) had no objects fastened to the strings. He called string pulling a 'self-rewarding behaviour'. The two birds we tested systematically for the importance of a reward clearly string pulled more readily when the thimble contained food then when it was empty. However, some individuals which perfectly mastered string pulling at times seemed to be obsessed in performing this behaviour even with an empty thimble. In addition, males 15 and 478 in our pilot test lifted the filled thimble in a quarter of times without eating. Thus, some individuals seem to perform string pulling at times for its own sake (just for fun), while a few other individuals clearly capable of string pulling did not show it most of the time. As an extreme, one male Goldfinch had shown a single perfect string pulling and holding already in the first solo session and repeated it twice in the third session; but it never did it again thereafter, neither in subsequent seven solo sessions nor in 10 sessions with a model bird. Obviously, more still unknown factors influence an individual's readiness to act.

Acknowledgements

We gratefully acknowledge the engaged technical assistance of N. Ballerstädt, U. Lauterfeld and E. Schülke during the experiments. M. and E. Schlag cared for the animals' daily welfare. We thank B. Knaur and T. Weber who spent much thought on preparing the graphs. Two referees made very helpful suggestions after reading the manuscript. With gratitude we welcome our birds' readiness to cooperate and uncover their personalities.

Literature Cited

Altevogt, R. 1954: Über das ,,Schöpfen'' einiger Vogelarten. Behaviour **6**, 147—152.

Bierens de Haan, J. A. (1933): Der Stieglitz als Schöpfer. J. Ornithol. **81**, 1—22.

Clark, G. A. 1973: Holding food with the feet in passerines. Bird Banding **44**, 91—99.

Dukas, R. E. (ed.) 1998: Cognitive Ecology: the Evolutionary Ecology of Information Processing and Decision Making. The Univ. of Chicago Press, Chicago/London.

Erhardt, A. 1933: Kritische Bemerkungen zu der Arbeit von Bierens de Haan ''Der Stieglitz als Schöpfer''. Z. Psychol. **130**, 393—398.

Fischel, W. 1936: Die Gedächtnisleistungen der Vögel. Z. Tierzücht. Züchtungsbiol. **36**, 13—38.

Gesner, C. 1669: ''Vogelbuch'' (Nachdruck 1981 in Schlütersche Verlagsanstalt Hannover). 71 pp.

Heinrich, B. 1995: An experimental investigation of insight in common ravens (*Corvus corax*). Auk **112**, 994—1003.

Heinrich, B. 2000: Testing insight in ravens. In: The Evolution of Cognition (Heyes, C. & Huber, L., eds). The MIT Press, Cambridge, MA; London, UK, pp. 289—305.

Herter, W. R. 1940: Ueber das ''Putten'' einiger Meisen-Arten. Orn. Monatsber. **48**, 105—110.

Hertz, M. 1926: Beobachtungen an gefangenen Rabenvögeln. Psychol. Forsch. **8**, 336—397.

Hinde, R. A. 1956: The behaviour of certain Cardueline F1 inters-pecific hybrids. Behaviour **9**, 202—214.

Koolhaas, J.M., Korte, S.M., De Boer, S.F., Van Der Vegt, B.J., Van Reenen, C.G., Hopster, H., De Jong, I.C., Ruis, M.A.W. & Blokhuis, H.J. 1999: Coping styles in animals: currents status in behavior and stress-physiology. Neurosci. Biobehav. Rev. **23**, 925—935.

Lorenz, K. 1939: Vergleichende Verhaltensforschung. Zool. Anz. Suppl. **12**, 69—102.

Millikan, G. C. & Bowman, R. I. 1967: Observations on Galápagos tool-using finches in captivity. Living Bird **6**, 23—41.

Perrins, C. M. (ed.) 1994: Handbook of the Birds of Middle East and North Africa, Vol. VIII. Oxford Univ. Press, Oxford, pp. 568—604.

Plinius, C. 1554: Historiae mundi Libri XXXVII. Johan.Feyerabendt, Frankfurt/M.

Seibt, U. 2002: Inter-individual variance in problem-solving of Goldfinches *Carduelis carduelis*. Zoology **105** (Suppl. V), 9.

Sokal, R. R. & Rohlf, F. J. 1981: Biometry, 2nd edn. W.H. Freeman and Co., San Francisco, CA.

Tebbich, S., Taborsky, M., Fessl, B. & Blomqvist, D. 2001: Do woodpecker finches acquire tool-use by social learning? Proc. R. Soc. Lond. B **268**, 2189—2193.

Teyrovský, V. 1930: A Study of Ideational Behavior of a Garden Warbler, *Sylvia borin* (Bodd.). Publ. De la Faculté des Sciences de l'Université Masaryk No.122.

Thienemann, J. 1933: Der Stieglitz als Schöpfer. Orn. Monatsber. **81**, 92—93.

Thorpe, W. H. 1956: Learning and Instinct in Animals. Methuen & Co, London, pp. 333—339.

Vince, M. A. 1956: ''String-pulling'' in birds. I. Individual differences in wild adult great tits. Br. J. Anim. Behav. **4**, 111—116.

Vince, M. A. 1958: ''String-pulling'' in birds. II. Differences related to age in greenfinches, chaffinches and canaries. Anim. Behav. **6**, 53—59.

Vince, M. A. 1961: ''String-pulling'' in birds. III. The successful response in greenfinches and canaries. Behaviour **17**, 103—129.

Wechsler, B. 1995: Coping and coping strategies: a behavioural view. Appl. Anim. Behav. Sci. **43**, 123—134.

Wood, D. 1989: Social interaction as tutoring. In: Interaction in Human Development (Bornstein, M.H. & Bruner, J.S., eds). Lawrence Erlbaum Assoc., Hillsdale, NJ, pp. 59—80.