

University of South Bohemia in České Budějovice

Faculty of Science

**Once bitten twice shy:
long-term behavioural changes caused by trapping experience in
willow warblers *Phylloscopus trochilus***

RNDr. Thesis

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Annotation: In this study, we provide an evidence that willow warblers captured into mist nets by using conspecific male playback avoided the playback and the mist net on future capture attempt. Whether the subsequent capture attempt was carried out within a same breeding season or in a following breeding season, the results were very similar suggesting that the situation is very strongly memorized by willow warblers. Such a behavioural changes leading to "trap shyness" could potentially affect population dynamics estimates and behavioural data based on playback captures or playback provocation in willow warblers but very likely in many other species as well.

Annotation (in Czech): V této studii dokládáme, že samci budníčka většího (*Phylloscopus trochilus*) se při druhém pokusu o odchyt do nárazové sítě s pomocí playbackové nahrávky chovají jinak než při prvním odchytu a vyhýbají se nárazu do sítě. Tato změna v chování v důsledku odchytu se projevila jak u samců, které jsme se pokoušeli znovu odchytit několik dní po prvním odchytu, tak i u samců, které jsme se pokoušeli znovu odchytit až v další hnízdní sezóně. Budníčci si tedy odchytovou událost pamatují dlouhodobě. Změny v chování způsobené odchytem - výbání se sítí a playbacku - mohou negativně ovlivňovat playbackové experimenty nebo populační studie, které spoléhají na data ze zpětných odchytů. Podobné změny v chování lze očekávat nejen u budníčka většího, ale i u dalších druhů.

Declaration (in Czech):

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své rigorózní práce, a to v nezkrácené úpravě elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejich internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

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Statment about the author's contribution to the study:

Pavel Linhart was the first and corresponding author of this study. PL was involved in all stages of the study. PL participated on study design, carried out the experiments and analysed the data, and he also substantially contributed to manuscript writing.

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Once bitten twice shy: long-term behavioural changes caused by trapping experience in willow warblers *Phylloscopus trochilus*

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In dangerous situations, animals learn from experience to anticipate risks during similar subsequent occasions. Mist netting may represent just such a dangerous occasion and may serve as a tool to get insight into whether and how memorizing and recognition of the circumstances that form the prelude to a recapture can alter the animal's behaviour after capture, as well as it may affect the subsequent recapture rates. We used a playback lure to study the capture latency in willow warblers *Phylloscopus trochilus*, both without any and with a previous capture experience (either in the same year or in a previous one). We found increased response latencies to the playback lure for experienced males, compared to naive males. Naive males responded faster in the presence of a mist net than without a mist net; while experienced males tended to increase their response latencies. Individuals with between-year capture experience showed exactly the same response pattern as individuals with a capture experience within the same year. These findings suggest that the birds may recall the capture event even a year later. It is very likely that the playback lure, with or without the net's presence, contributed significantly to the apparent risk of detection. We believe our study reveals that long-lasting modifications of behaviour induced by capture and handling deserve further attention, as they might have a serious impact on the value of behavioural and ecological data, which is either based upon observing captured individuals and/or upon the recapture rates.

Animals typically face a lot of variation and change in their environmental and social conditions. Flexible response strategies, mediated by learning, often yield better pay-offs than fixed behavioural patterns because of the unpredictable nature of opportunities and the risks in life. For example, birds may remember and revisit particularly rich feeding sites (Mettke-Hofmann and Gwinner 2003) or migratory stopover sites that have proven to be safe on previous occasions (Minias et al. 2010). Birds can not only learn from a positive experience, but also quickly learn from a negative experience with for example inedible prey (Exnerová et al. 2010), frightening persons (Levey et al. 2009, Marzluff et al. 2010), or nest disturbances (Lord et al. 2001, Chen et al. 2011). Especially, avoidance behaviour or increased vigilance learnt by experiencing stressful events, such as real or simulated predator encounters, seems to be a common phenomenon that may directly benefit individual survival and reproductive success (reviewed by Curio 1998).

Quick memorization of specific conditions and cues that accompany stressful situations is often critical due to the short nature of such situations, and due to the fact that every additional exposure to a similar situation might be fatal. Many animals, including birds, are indeed able to quickly memorize frightening situations, even after a single or only a few exposures; while specific stimuli can trigger the

appropriate response even months after the learning exposure, as revealed by the studies of fear conditioning and social learning about predators (Chivers and Smith 1998, Fendt and Fanselow 1999, LeDoux 2003, Griffin 2004 for review). Different modalities can all play a role in memorization of the first occurrence and recognizing subsequent reintroduction of threatening situations. Birds can rely on both visual as well as acoustic cues (reviewed by Griffin 2004). Starlings *Sturnus vulgaris*, for example, will avoid an owl model (*Bubo bubo*) if they have seen it with a struggling conspecific in its talons before (Conover and Perito 1981), and blackbirds will quickly learn to avoid predators if their presence is associated with conspecific alarm calls (Vieth et al. 1980).

Many human activities can be stressful to animals, including the capturing and ringing of wild birds. Thousands of amateur and professional ornithologists ring millions of birds every year all over the world (see e.g. <www.bto.org>, <www.pwrc.usgs.gov/bbl>). Capturing and ringing are the main sources of data on the survival and migration of birds, and it allows us to mark individuals for studies that require identity labels. Mist netting, which is probably the most common technique used to capture birds for ringing, is generally not considered to be harmful (Bart et al. 2001, Spotswood et al. 2012; but see Amat 1999); however,

there are strong indications that the capture is perceived as a stressful experience by the birds. Levels of stress hormones increase in response to capturing and handling (Wingfield et al. 1982), and the birds may need significant recovery time before resuming activities, focus, and alertness at the same levels as before the event. Sometimes birds may even leave their territories after the capture (Legare et al. 1999).

We believe that the event of a bird being captured and released by humans might in many ways reflect the event of a bird being caught by a predator with a subsequent escape. Chasing and capturing birds by humans has already been successfully used as a simulated predator encounter in laboratory studies of socially transmitted fear responses (Griffin and Boyce 2009). Consequently, we believe mist netting and the subsequent handling of birds has an overlooked potential to be used as a tool to study the direct acquisition of predator avoidance behaviour (Griffin 2004). Importantly, the capture experience could also cause behavioural changes which may well affect the results of specific studies. Capture avoidance can influence recapture rates, and hence the population and survival estimates (Pradel 1993). Besides recapture rates, various other behaviours that are relevant to investigators could be affected by the capture experience. However, we currently have only a few detailed studies on the lasting consequences of the brief, but inherently stressful, treatment of study animals.

In this study, we investigated adult male willow warblers *Phylloscopus trochilus* in order to evaluate whether the capture using playback lure causes behavioural changes in the period preceding the following capture attempt. We addressed these questions: 1) are male willow warblers, captured by using a playback lure, more difficult to catch subsequently than are naive males in a capture attempt (both within and across breeding seasons)? 2) If so, what cues do the males use to anticipate the dangers associated with the capture? To answer these questions, we assessed the response latency of males with and without any previous capture experience. We considered the conditions at two capture stages as cues: the playback lure of a conspecific song (with the inherent presence of a mist netter), as well as the presence of a mist net.

Methods

Study site and population

Our experiment was conducted from 29 April to 21 May in 2010, at a wooded marshland of about 1 km² size, near the town of České Budějovice (48°59'44"N, 14°26'23"E), South Bohemia, Czech Republic. The area consists of ponds and marshy areas with stands of willow *Salix* spp., birch *Betula* spp., and aspen *Populus* spp. trees, as well as some old oak *Quercus* spp. avenues along the edges. This small area hosts a relatively numerous population of willow warblers due to the optimal environmental conditions. The estimated population is about 60 breeding pairs each year. We have been continuously ringing and colour ringing the males within the area since 2007. The number of all ringed males (either newly ringed males or males that have been re-sighted) within the area in each

year were: 2007 – 17, 2008 – 40, 2009 – 50, and 2010 – 52. There always were some non-ringed males breeding (the remainder enough to make the estimated total 60 males). The proportion of males returning to the area is quite high. From 88 ringed males during the years 2007–2009, 38 males were re-sighted during 2008–2010 (= 43%).

Experimental groups and set-up

We distinguished between the groups of males according to their capture history. Naive males (labelled N; n = 24) had never been captured before 2010, and most probably included two-year-old males, as well as some older males with a breeding history outside the study area. Experienced birds had been captured and ringed in previous years (2007–2009) and consisted of at least three-year-old males from the study area (they were labelled EB – ‘experienced between years’, n = 27; consisting of 18 at least 3 yr, 7 at least 4 yr, and 2 at least 5 yr). The interval between the capture and recapture attempt was at least 310 d. All of the experienced males were captured by using a playback lure, and handled in a similar manner as were the birds in 2010. In addition, we tried to recapture 20 of the N males within the same year after the first successful capture (this subset of N were labelled as EW – ‘experienced within year’ – males with capture experience within the last year 2010; n = 18), in order to find out whether the between-year recaptures would yield similar results as the within-year recaptures. Two out of 20 males were not re-sighted at all, which could be due to relocation or death of these males (for which we have no indication that it could be related to the capture experience). All naive recapture attempts (EW) were carried out within a month after the first capture event (1st captures: 29 April–19 May; 2nd captures: 19 May–21 May).

For all three groups, the experiments were carried out in the morning between 6:00 and 12:00, and there were no differences in experiment timing between the groups (Kruskal–Wallis test: $H = 1.09$, $DF = 2$, $p = 0.581$). EW males were tested within three days after all experiments with the N and EB males had been completed. Therefore, there was a difference in the experimental dates between the groups (Kruskal–Wallis test: $H = 39.254$, $DF = 2$, $p < 0.001$). However, N and EB males did not differ in their experimental dates (Mann–Whitney U test: $W = 360$, $n_N = 24$, $n_{EB} = 27$, $p = 0.500$). Males from the N and EB groups were randomly selected for the experiments, and were evenly dispersed between the experimental dates and times. Experiments were not performed on either rainy or windy days. All males were paired and their mates were either incubating or rearing.

The experiment always consisted of two stages for each individual: playback and capture. These two stages differed in the set of cues that might be used by willow warbler males to anticipate the capture situation: first, we tested the effectiveness of playback to attract the bird into a target flight trajectory in playback stage. Immediately after the playback stage, we added the mist net into the flight trajectory to assess playback response to both playback and mist net cues being present in capture stage. All experiments were done by the same person (PL), who also did all the mist netting in previous years. PL wore the same type

of green-black field outfit during all years when the males were captured.

Playback stage

The playback stage always preceded the capture stage. First, we selected the place inside the territory for playback, and to place the mist net later on. We placed the loudspeaker well inside the territory, close to the bird's singing posts (these were known from a territory mapping and about a five minute observations right before the start of the experiment). We always tried to place the loudspeaker between two low bushes, so that it could provide shelter and allow the males to descend close to the ground and to fly over the loudspeaker. This was not possible with male no. 1046, who bred in dense young trees with leafless bottom twigs. We used a single recording of a singing willow warbler as the playback lure throughout the years, including the 2010 experiments. It was a high quality (no other birds, and no background noise in the recording) recording of a male coming from the study area (recorded in 2005), and consisted of 6 different songs (song rate: 6 songs min^{-1}) that were played back in a loop during the experiments. Playback trials lasted until a male responded (by flying over the loudspeaker at a height of 1.5 m – implying that it would have been captured if the net would have been present). We scored the latency to response. If a male did not respond within 600 s (10 min) of playback we stopped the trial and assigned a latency of 600 s to that particular individual.

Capture stage

After the playback stage was over (male either responded or allocated time of 600 s ran out), we built a 3×2.5 m mist net into the expected flight path (which took approximately 2 min) before starting the playback again for the capture stage. We again played back the lure song until the male responded (= successful capture), or for 600 s (unsuccessful capture). Again, we scored the latency to response. Captured males were ringed (aluminium ring + unique combination of up to three colour rings) and we measured their basic body parameters. The males were always released in good condition within 5 min after capture.

Statistical analyses

We used the Cox proportional-hazards regression ('coxph' function from the R 'survival' package) to analyse the response latencies, as there were a large number of right censored observations (i.e. the individual did not respond within 600 s of the experiment, and therefore the observation was stopped) for the EB and EW groups. Whenever we compared survival between the playback and capture stages, we used the 'frailty' argument to code for observations from the same individuals. This argument allowed us to account for an individual's variation in response latencies in a similar manner as by using individuality as a random effect in the linear mixed effect models (Therneau et al. 2000). We asked whether the group (N, EB, EW), stage (playback, capture), or interaction of the group and stage effected the response

latency. We ran three regression analyses in order to compare three possible group combinations: N vs EB, N vs EW, and EW vs EB. We used a Bonferroni correction for multiple testing (each group was used in two tests; therefore, the corrected α -level was $0.05/2 = 0.025$). We preferred this alternative rather than one model with all three groups at once because the groups were not independent (EW was a subset of N males), and the model would not be well balanced; some of the N males were tested 4 times (playback/capture first as N, and second as EW), while the EB and the rest of the N were tested only twice. When we found an interaction effect, we did 4 pairwise comparisons of each combination of levels (group/stage).

All captured N males were used in comparison with the EB. Only those N males who were tested as EW were used for comparisons with the EW. There was a single naive male that we had attempted to capture, but could not. We did not include this male in the analyses because the EB as well as the EW males were only recruited from males that were captured within 600 s.

Although tests for all three groups were carried out in comparable time of day, and N and EB males also on comparable dates, we tried to test whether time (number of minutes from 6:00) or date (number of days since first day of testing) could influence the response latencies in the N, EB, or both groups. However, there was no effect of time or date for either of the groups alone, or for both groups combined (all $p > 0.15$) so we did not include these parameters in the models.

In order to try to assess the impact of age on response latency, we further divided the experienced males into three age classes, and tried to compare the response latencies of the at least 2 yr old males (2 yr+, $n = 18$, all of the EW), with at least 3 yr old males (3 yr+, $n = 18$, subset of EB); and at least 4 yr old males (4 yr+, $n = 9$, the rest of EB). We again used the Cox PH regression.

Results

In general, there was a similar pattern in response latencies of EW and EB males. Fewer males responded (in the playback stage already) in both experienced groups, and those who had responded hesitated longer when compared to the N males. There was also a tendency for EW and EB males to respond better during the playback stage when the mist net was not present. On the other hand, N males responded better in the capture stage when the mist net was present. In experienced males (EW, EB), there was no effect of age class (2 yr+, 3 yr+, 4 yr+) on the response curve, either in the playback stage (Cox PH regression: $\chi^2 = 1.88$, $DF = 2$, $p = 0.391$), or in capture stage (Cox PH regression: $\chi^2 = 0.69$, $DF = 2$, $p = 0.708$).

Naive males (N) vs males with between year capture experience (EB)

There was significant effect of the group (N, EB) and group:stage interaction upon the response latencies of the N and EB males. The effect of the stage (playback/capture) on response latencies reached marginal significance (Table 1).

Table 1. Cox PH regression results for the pair comparisons of the three groups. Significant effects are emphasized in bold. Effects significant after Bonferroni correction for multiple comparisons (corrected α -level = 0.025) are accompanied with an asterisk.

	Coefficient (β)	SE	Wald χ^2	p value	Risk ratio	95% CI
N vs EB						
group (N)	2.05	0.49	17.20	< 0.001*	7.76	2.94 to 20.446
stage (capture)	-0.84	0.46	3.41	0.07	0.43	0.18 to 1.05
group:stage	2.03	0.58	12.42	< 0.001*	7.62	2.46 to 23.61
N vs EW						
group (N)	2.13	0.49	19.20	< 0.001*	8.39	3.24 to 21.74
stage (capture)	-0.35	0.54	0.40	0.52	0.71	0.24 to 2.06
group:stage	1.19	0.66	3.28	0.07	3.30	0.91 to 12.05
N vs EW (without the individual no. 1046)						
group (N)	2.27	0.53	18.53	< 0.001*	9.73	3.45 to 27.39
stage (capture)	-0.38	0.59	0.42	0.52	0.68	0.22 to 2.17
group:stage	1.67	0.72	5.36	0.02*	5.31	1.29 to 21.85
EB vs EW						
group (EW)	-0.38	0.71	0.28	0.59	0.68	0.17 to 2.77
stage (capture)	-1.00	0.48	4.32	0.04	0.37	0.14 to 0.95
group:stage	0.64	0.75	0.73	0.39	1.90	0.44 to 8.21

Only the group and interaction effects remained significant after a Bonferroni correction (corrected α -level = 0.025). The N males responded better than the EB males in both stages. The interaction effect was caused by the fact that the N males responded better during the capture stage (Cox PH regression: $\beta = 1.19$, Wald $\chi^2 = 11.3$, $p < 0.001$); while EB males tended to respond better in the playback stage. (Cox PH regression: $\beta = -0.91$, Wald $\chi^2 = 3.78$, $p = 0.052$) (Fig. 1a.)

Naive males (N) vs males with within-year capture experience (EW)

Again, there was a significant effect of group (N, EW) on the response latencies of the males. The stage (playback, capture) had no effect on response latencies. The interaction between group and stage was marginally significant. After a Bonferroni correction, only the effect of the group remained significant (Table 1). Again, the N males responded better than the EW males in both stages. We consider that the interaction between group and stage was not significant, due in part to the reduced sample size, and due partly by the fact that there was no difference in the response latencies of the EW males during playback and capture (Cox PH regression: $\beta = -0.45$, Wald $\chi^2 = 0.56$, $p = 0.450$); although fewer EW males responded in the capture stage, in a manner similar to the EB males. The N males still responded significantly better in the capture stage than in the playback stage (Cox PH regression: $\beta = 1.02$, Wald $\chi^2 = 6.43$, $p = 0.011$). As visible from the survival curves (Fig. 1b), a single N male (male no. 1046) responded much later during the capture stage than did the rest of the males. He also responded very late in the playback stage (the second greatest latency of the N males). The reason for his unusual response could be that he was the only male that lacked low bushes in his territory in which we could place the loudspeaker. His response might therefore be hindered due to the missing bush cover around the loudspeaker. The dropping of this observation causes a remarkable change in the regression coefficients, compared to other observations (standardized dfbeta = -0.274; median

standardized dfbeta for all observations = 0.019). When we removed this male from the analyses, the interaction of the group and stage became significant even after a Bonferroni correction (Cox PH regression: $\beta = 1.67$, Wald $\chi^2 = 5.36$, $p = 0.021$; corrected α -level = 0.025).

Males with within-year (EW) vs males with between-year (EB) capture experiences

Only the stage affected response latencies when comparing EW and EB males (Table 1). However, this significant effect becomes only a trend after controlling for multiple comparisons. Both groups together tended to respond better in the playback stage, compared to the capture stage; the opposite result that we got with the N males. The two groups did not differ at any stage.

Discussion

In this study, we have shown that willow warblers with capture experience are more difficult to capture into a mist net using a playback lure in the second capture event. This is true if the males encounter the second capture attempt within a period of days or weeks, as well as for encounters occurring about a year after the initial capture. Playback without the presence of a mist net was already sufficient to reduce the response dramatically. Males with previous capture experience showed a tendency for a further reduction in response during the capture stage in the presence of the mist net, compared to the playback stage. In contrast, naive males responded even faster the second time with a net than the first time without a net.

Reduced recapture rate

Previous capture experience has been reported previously to have an impact on the recapture rate in a wide variety of species. For example, Wegge et al. (2004) reported a decrease in camera capture–recapture rates of tigers *Panthera tigris* in their study. Within the first 5 nights, all 9 tigers in their

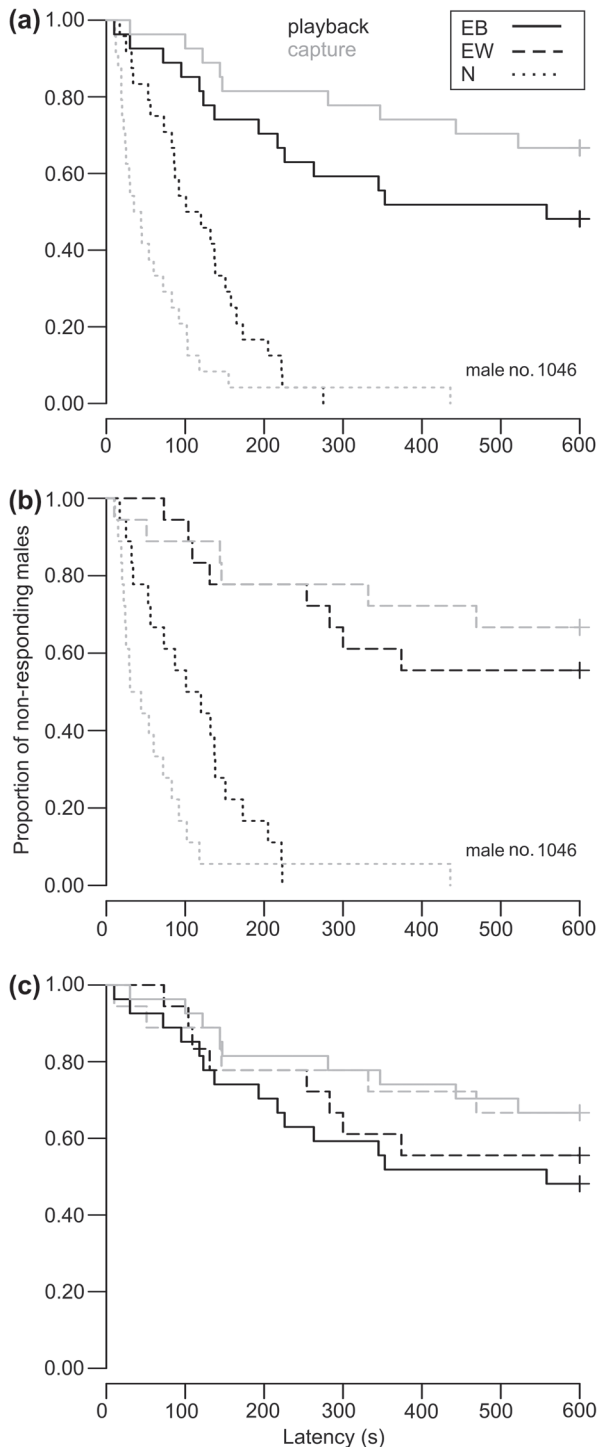


Figure 1. Pair comparisons of survival curves (i.e. response latencies) for the three groups of males (EB – solid line, EW – dashed line, N – dotted line) during 600 s of playback (black) and capture (grey) stages. The exceptional response of male no. 1046 is highlighted.

study area had been captured, while on the following nights the numbers decreased to 4 (nights 6–10) and 3 (nights 11–15). Dunnet and Ollason (1978) recaptured only 53% of the northern fulmars *Fulmarus glacialis* which had been captured in hand nets during the preceding year and which were known to still be alive. Interestingly, the opposite

is also possible: an increase in recapture rate compared to the first-time capture rate. For example, Tyrrell et al. (2009) showed that snakes can show ‘trap happiness’, which is probably due to using baited traps that might make the traps attractive for revisiting.

In contrast to our findings, there was no evidence for capture avoidance (see trap dependence; Pradel 1993) in many earlier studies on small passerines; including for example one nest-box recapture study in blue tits *Cyanistes caeruleus* (Blondel et al. 1992), and a mist net recapture study on eight warbler species, including the willow warbler (Salewski et al. 2007). The discrepancy between these studies and our own might be explained by the different capture methods that were used in these studies. We used playback to lure the birds into the mist nets, while Blondel et al. (1992) caught breeding birds in front of nest-boxes, and Salewski et al. (2007) set up a constant effort mist-netting site.

Song playback could provide the birds with more cues about the upcoming dangerous situation, and thus increase the negative trap effect. Nevertheless, our results clearly show that relatively short-lived songbird species also can use previous experience to adjust their vigilance in memorized risky conditions. Moreover, the experience can shape their behaviour at least for about a year. These insights may be widely accepted and expected by bird ringers that have experience with recaptures or re-sightings (which is often an advantageous method, allowing getting more accurate estimates of marked males than recapture). However, we are unaware of any published report on this phenomenon or a quantification of bird behaviour that explains the capture-dependent recapture efficiency. More studies should be carried out to see whether the response is specific to willow warblers or is more widespread among species.

Independent of whether it is a first or second attempt to catch a particular individual, capture success may already vary from a large number of intrinsic and extrinsic factors. Capturing may be more or less successful depending on, for example, weather conditions (Lukas et al. 1996), habitat characteristics (Harrison et al. 2000), or personality (Garamszegi et al. 2009). However, we believe our results are not confounded by such environmental factors as all of the experiments took place in the same location for which the habitat did not change between years. Furthermore, our capture experiments were randomly spread within a testing period as well as done at the same time of the day and these variables did not seem to affect the response latencies; therefore, we believe our results are not confounded by environmental factors.

A potentially confounding parameter in our study may be age (which we were not able to assess as moulting patterns prevent accurate aging of willow warblers by plumage (Jenni and Winkler 1994)). Theoretically, age could have had a significant impact on the response rate. Older individuals of the ortolan bunting *Emberiza hortulana* have been found to respond more intensely to the playback of a conspecific song, compared to younger individuals (Osiejuk et al. 2007); and older great tits turned out to be faster explorers than younger great tits (Carere et al. 2005). Therefore, if age would have played a similar role in our willow warbler study, we would have expected stronger responses

and thereby higher capture rates for the E males than for N males; the opposite of what we found, even though little data is available with which to make generalized statements about the effects of age on playback responsiveness. We did not find any effect of age when comparing age classes of the experienced males. Moreover, the same N males twice caught in the same season showed a highly similar pattern to the between-year data during the second capture attempt, suggesting that age is indeed not an important factor.

Important cues for capture event recognition

It has been shown previously that birds can quickly memorize acoustic stimuli and that they are especially capable of learning the details of conspecific songs (Chew et al. 1995, Mello et al. 1995). A study in zebra finches *Taeniopygia guttata* had shown that female birds can memorize and use familiar songs during song preference tests several months after the exposure to these songs (Riebel 2000); a study in great tits had shown that female birds can even learn to distinguish minute voice differences between their mate and their neighbour singing exactly the same song type (Blumenrath et al. 2007). In addition, territorial male birds are often capable of distinguishing between neighbours and strangers (reviewed by Stoddard 1996), and further are reported to remember the songs of their neighbours from the previous year (Godard 1991). Therefore, we contend that recognition of playback conditions, potentially including the individual song features of our stimulus recording have contributed to reduced catching rates of experienced birds. This interpretation is congruent with studies that have shown that animals can quickly memorize acoustic stimuli associated with negative conditions leading to stress, fear, or pain (Curio et al. 1978, Young and Fanselow 1992, Mineka and Cook 1993, Quirk et al. 1995).

Although the presence of playback had an impact on capture avoidance in our willow warbler males, we can not separate it from the impact of the presence of the mist netter. Males seemed not to escape or hide in the presence of the mist netter alone nor did they give alarm calls or did they show any other sign of discomfort. However, the presence of the mist netter could also have had an influence, reducing the response of experienced males in the playback stage, as the mist netter was also always present in the playback stage. Several recent studies have shown that birds can quickly remember threatening persons (northern mockingbirds *Mimus polyglottos* – Levey et al. 2009; American crows *Corvus brachyrhynchos* – Marzluff et al. 2010; black-billed magpies *Pica pica* – Lee et al. 2011). Experiments comparing response latencies to different playback songs in the presence of the usual mist netter vs a harmless person could clarify whether willow warblers use the playback song, the mist netter, or both as cues for recognition of a capture situation.

The addition of the mist net itself was associated with an even better response in the naive but not in the experienced males, which might seem to be a counterintuitive result. However, this particular finding may be explained by an order effect. The capture stage was always second, and therefore the males were first attracted and stimulated in the playback stage. Based on their behaviour (high singing rate,

close proximity to loudspeaker), they remained agitated until the playback was started again in the capture stage after the building of the mist net about two minutes later. The presence of the mist net, only recognizable as a threat to experienced males, may explain the discrepancy in the response latencies between naive and experienced birds, as this was the only factor that changed between the two experimental stages.

Conclusions

Our study revealed behavioural changes due to the capture experience in willow warbler males. We showed that the males can memorize the conditions of the first capture event, which enables them to recognize similar conditions of a subsequent capture attempt and help them to avoid to be recaptured. Proper evaluations and greater insights into the behavioural changes caused by capturing may help to further improvements in demographic models, and has implications for behavioural studies that use captured-marked animals. Consequently, experimenters should plan their experiments paying special attention to possible behavioural changes in their study subjects due to the capturing. Furthermore, we suggest that capture experience imitates predator exposure (or similarly stressful and threatening situations) and could therefore serve as a tool to study the evolution and underlying mechanisms of predator recognition.

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