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RRH: *Apomorphine as an Emetic for Songbirds*

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Apomorphine as an emetic for insectivorous songbirds: effectiveness and post-release effects on survival and mass change

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ABSTRACT. Emetics can be used to obtain food samples from birds, but they can harm birds during or after treatment. Studies to date suggest that apomorphine is a safe emetic, but information is needed about possible post-release deleterious effects on birds. During one breeding season (March – July 2012) at a marshland in Spain, we collected food samples from insectivorous songbirds using apomorphine. We treated 67 Moustached Warblers (*Acrocephalus melanopogon*), 56 Reed Warblers (*A. scirpaceus*), 15 Great Reed Warblers (*A. arundinaceus*) and 12 Savi's Warblers (*L. luscinoides*). Effectiveness in inducing regurgitation was high (76.7%) and varied with species, being significantly more effective on Reed Warbler (91.1%), possibly because of morphological and physiological differences between case species which influenced the sensitivity to the emetic. No birds died during treatment. To check for possible post-release negative effects, we considered 53 treated Moustached Warblers and 37 treated Reed Warblers and selected an equal number of untreated individuals (simply identified, banded and measured). We found no support for differences in survival or recapture probabilities between the treated and the untreated set in any of the two species within 21 days after administering apomorphine. We calculated body mass changes of all subsequently recaptured (within 21 days) Moustached Warblers and we found no differences between treated ($N = 8$) and untreated ($N = 22$) birds, suggesting normal foraging activity after release. The results suggest that apomorphine is a safe emetic, without negative effects on survival at least in the short term. The effectiveness we obtained using apomorphine with insectivorous songbirds contrasts with some of the previous studies and confirms the occurrence of differences in effectiveness among different taxa of songbirds. Similarly to the differences between our case species, this variability in sensitivity to the emetic could be caused by morphological and physiological differences between taxa.

Key words: bird diet, capture-recapture analysis, Cormack-Jolly-Seber model, Moustached Warbler, Reed Warbler

Emetics have been used by many investigators to study the diet of wild birds (e.g., Rosenberg and Cooper 1990, Poulin and Lefebvre 1995, Carlisle and Holberton 2006).

Effectiveness in inducing regurgitation and safety of different emetics can be influenced by many variables such as dosage, bird size, bird species, stress during handling and amount of food in the digestive tracts (Lederer and Crane 1978, Díaz 1989, Poulin et al. 1994, Poulin and Lefebvre 1995, Durães and Marini 2003, Diamond et al. 2007).

Antimony potassium tartrate is a widely used emetic (Durães and Marini 2003) found to be effective at inducing regurgitation (60.5 – 89.8% of treated birds; Poulin and Lefebvre 1995, Johnson et al. 2002, Durães and Marini 2003, Lopes et al. 2005, Carlisle and Holberton 2006). However, several investigators have also reported negative effects of this emetic on songbirds. For example, Zach and Falls (1976) reported mortality rates ranging from 12.5% to 50%, and Carlisle and Holberton (2006) reported that 1.5% of free-living birds and 94.4% (17 of 18) of captive Dark-eyed Juncos (*Junco hyemalis*) died after receiving the emetic. Poulin et al. (1994), treating a wide range of bird species, found an inverse relationship between mortality rate and body mass (higher mortality in birds smaller than 10 g) and significantly higher mortality in birds regurgitating only liquids (i.e., with empty digestive tracts). However, the relationship between body size and mortality has not been confirmed by other studies (Poulin and Lefebvre 1995, Durães and Marini 2003). Poulin et al. (1994) observed that lowering the concentration of the emetic reduced mortality of some especially sensitive small species (Yellow-chinned Spinetail *Certhiaxis cinnamomea* and Bananaquit *Coereba flaveola*). Similarly, Poulin and Lefebvre (1995) found that lowering the concentration of the emetic reduced the mortality rate of some Manakins species, but also reduced the proportion of birds that regurgitated, and Johnson et al. (2002) obtained effectiveness reduction with American Redstarts (*Setophaga ruticilla*) by lowering the concentration of the emetic. Others studies have not reported mortality. Zduniak (2005) obtained no mortality treating nestlings of Hooded Crow (*Corvus corone cornix*), a heavy-size songbird, and assumes that the administration of a 5% glucose solution after the treatment caused the lack of negative effects. Similarly, Tomback (1975) obtained no pre-release mortality using tartar emetic on songbirds, but only 23 individuals were treated.

Information about post-treatment deleterious effects (death caused by the emetic, abandonment of the area) in the wild is contradictory: Johnson et al. (2002) reported significantly lower resighting rates of treated than of untreated birds (61.5% vs. 13.2%) for three species of warblers, whereas Poulin et al. (1994), Durães and Marini (2003), and Carlisle and Holberton (2006) did not find significant differences between return rates (proportion of marked individuals released that are recaptured) of treated birds and untreated birds (but see further details in the Discussion). The abandonment of the area due to the stress of treatment could be a cause of lower resighting or return rates: Poulin et al. (1994) suggest that the stress associated with the administration of the emetic led many birds to leave the area and hypothesize that mortality and desertion were both causes of lower (although not significant) return rates of treated birds.

Given these negative effects, investigators using emetics to study the diets of wild birds would benefit from a safer alternative. Other substances proposed for use as emetics include ipecachuana, lukewarm water, and apomorphine. Ipecachuana is a natural extract from the roots of rubiaceus plants (*Cephaelis ipecacuanha* or *C. acuminata*; Diamond et al. 2007). Diamond et al. (2007) report no mortality using this emetic on songbirds and suggest that its dosages are less likely to reach a toxic level than tartar emetic. Investigators studying food habits of songbirds by flushing stomachs with lukewarm water have reported either no mortality (Ford et al. 1982) or very low mortality rates (0.36%, Jenni et al. 1990), and no significant differences in return rates of treated and untreated birds (Ford et al. 1982, Jenni et al. 1990).

Apomorphine acts by stimulating the vomit center via the chemoreceptor trigger zone in the fourth ventricle in the bulb of the spinal cord (Chaney and Kare 1966). Investigators using apomorphine have reported effectiveness ranging between 43.7 and 71% (Schluter 1988, Díaz 1989, Valera et al. 1997) and no mortality of birds prior to release (Schluter 1988, Díaz 1989, Valera et al. 1997, Poulin et al. 2002, Mwangomo et al. 2007), while the only reported mortality cases are three Serin (*Serinus serinus*) nestlings of the same nest (of 110 treated nestlings of granivorous songbirds), which were encountered dead after treatment, plus one young Goldfinch (*Carduelis carduelis*) which died from asphyxia by failing to regurgitate big seeds (Valera et al. 1997). Such results suggest that apomorphine is a safe emetic, but information is needed about possible post-release deleterious effects on birds. Furthermore, the effectiveness of apomorphine in inducing regurgitation by insectivorous birds has not yet been clearly assessed. For example, apomorphine was found to be ineffective with Blue Tits (*Parus caeruleus*) and Great Tits (*P. major*) (Pulido and Díaz 1994, Valera et al. 1997), whereas Poulin et al. (2002) obtained food samples using apomorphine with Bearded Tits (*Panurus biarmicus*) and Reed Buntings (*Emberiza schoeniclus*). Mwangomo et al. (2007) used apomorphine successfully with Superb starlings (*Lamprotornis superbus*) and unsuccessfully with three partially insectivorous Weavers species.

Our objective was to assess the impact of using apomorphine on several insectivorous songbirds, including Great Reed Warblers (*Acrocephalus arundinaceus*), Reed Warblers (*A. scirpaceus*), Moustached Warblers (*A. melanopogon*), and Savi's Warblers (*Locustella luscinoides*). Additionally for the Moustached Warbler and the Reed Warbler we compared the survival, recapture probabilities, and mass of treated and untreated birds to provide further information about the effectiveness and safety of this emetic.

METHODS

Field work took place at the Pego-Oliva Natural Park (38°52' N - 0°04' W, Spain) from 23 February to 5 July 2012. This coastal marshland (1250 ha) is located between the provinces of Valencia and Alicante, and includes large areas of reedbeds dominated by *Phragmites australis* and *Thypha angustifolia*, rice fields, and water bodies (Urios et al. 1993, Generalitat Valenciana 2010).

We captured birds daily using six mist nets (10 m, 60-mm mesh) at one of 10 capture stations. Captures started 30 min before dawn and ended 4 h later. During normal banding activity, captured birds were banded, measured, aged, sexed when possible (Svensson 1992), weighed, and released.

During each of four periods (15 - 23 March, 10 - 30 April, 31 May - 7 June, and 2 - 5 July), we collected food samples until we had treated at least 15 birds of each of the most common species (Moustached and Reed warblers). During each period, captured birds were banded, aged, and sexed, then two drops of a fresh saturated solution of apomorphine (0.04 g of hydrochloride hemihydrate per ml of water) were placed on each eye with a 1-ml pipette; birds were then held until the liquid was totally absorbed (~5 min; Valera et al. 1997, Poulin et al. 2002). Birds were placed in a small, dark box lined with absorbent paper for 20 min (Valera et al. 1997), and we then measured and released them. We used apomorphine solutions for just three days to avoid potential loss of effectiveness (Díaz 1989) and checked for possible changes in effectiveness over time. We did not treat females that had brood patches to avoid possible harmful impacts; other individuals were also not treated either due to logistical problems (e.g., running out of apomorphine) or because we already had an adequate number of food samples. Untreated birds and those captured before and after the food sampling period constituted the untreated set. These birds were simply banded, measured, aged, and sexed (when possible); they were not subjected to a real control procedure (i.e., putting two drops of distilled water on each eye and keeping them in the box for 20 min) due to logistical problems (e.g., too many birds to treat given the long procedure) and because we wanted to minimize possible negative impacts on captured birds. Therefore, treated birds were manipulated longer (~5 min to administer the emetic and 20 min in the box), with the consequent additional stress, than our untreated birds. A chi-square (χ^2) test of independence was used to test for possible differences among species in the effectiveness of the emetic. Working on 2x2 contingency tables, chi-square values were subjected to Yates correction for continuity to avoid inflating Type I errors (Zar 2010). Apache OpenOffice Calc 3.4.1 (OpenOffice.org 2012) was used to perform the tests.

The possible effects on effectiveness of time since the apomorphine solution was prepared and time of capture were tested by fitting a saturated log-linear model to the three-way contingency table generated by the factors apomorphine effect (inducing regurgitation or not, 0/1), time since preparing the solution (first, second, and third day, corresponding to ~15 h, 39 h, and 63 h post-preparation, respectively), and time of capture (0 - 1.5 h, 1.5 - 3 h, and > 3 h after opening mist nets; Díaz et al. 1999). We could not include species as a factor in the model because that would have multiplied the number of cells by four, making the analysis unreliable. We used IBM SPSS Statistics 19.0 (Norušis 2011) to conduct the analysis.

To analyze possible differences in survival or recapture probabilities of treated and untreated birds, an untreated set was created for each species by selecting an equal number of untreated birds captured during the same period. We only considered Moustached and Reed warblers because sample sizes for the other two species were small (*N* < 15). We did not include the last sampling session (July), given the lack of succeeding capture activity. We considered only recaptures from 1 to 21 days after capture to standardize the capture effort. Over the 21-day period, captures were grouped into seven-day periods. This provided four capture periods: first capture, and recaptures during the first, second, and third weeks after the first capture. We analyzed capture-recapture data using models for open populations based on the Cormack-Jolly-Seber model (e.g., Lebreton et al. 1992). These models produce survival estimates that are not influenced by variation in recapture probability. Hence, they are more reliable than those based only on return rates (Martin et al. 1995). Data were analyzed using MARK 5.1 software (White and Burnham 1999). The starting model was a model with time and group effects (treated vs. untreated) in both survival and recapture probabilities. The set of *a priori* models included all the possible models from the starting model to a model with constant survival and recapture probabilities (25 models). To determine if the data fulfilled the assumptions of the CJS model, we used the bootstrap goodness-of-fit test approach (1000 simulations). Bootstrap results were used to estimate overdispersion factor $\hat{c}$ (Burnham and Anderson 2002). Model selection was done using the corrected Akaike Information Criterion (AIC_c ; see Burnham and Anderson 2002). We considered differences in AIC_c to indicate a real difference in the fit of the model to the data. We used model averaging to cope with model selection uncertainty. We used the Contrast program (Hines and Sauer 1989) to compare survival estimates.

To further assess the possible impact of apomorphine, we compared the change in mass of all treated and untreated Moustached Warblers that were subsequently recaptured and re-weighted within 21 days. For analysis, we used a repeated-measures ANCOVA with body mass as the repeated measure (mass at first capture and mass at recapture), treatment as the fixed factor, and tarsus length as the covariate to account for bird size. We used IBM SPSS Statistics 19.0 (Norušis 2011) to conduct the analysis.

RESULTS

Of 150 birds that received the emetic, 115 (76.7%) regurgitated (Table 1). Four birds regurgitated only liquid, suggesting their stomachs were empty. To assess the usefulness of food samples, we performed a preliminary analysis examining 19 samples from Moustached and Reed warblers. The mean mass of samples was 0.0029 ± 0.0031 (SD) g. We identified 6320 food fragments, with 2134 (34%) determined to be part of an organism (e.g., head, leg, antennae, thorax, or abdomen); unidentified fragments could not be identified as one of these parts. Using identified fragments, we identified all ingested arthropod prey and classified them to the order level.

No treated birds died, and all flew away when released. The emetic was more effective at inducing vomiting by Reed Warblers (51 of 56, 91.1%; Table 1) than by the other three species ($\chi^2_1 = 9.1$, $P = 0.0025$) and Moustached Warblers ($\chi^2_1 = 7.9$, $P = 0.0049$).

The results of fitting a saturated log linear model (Table 2) show no significant interaction between effectiveness of the emetic and either time of capture or time since the apomorphine solution was prepared. All main effects (Effect, Time, and Day) were significant (Table 2), reflecting the high effectiveness of the emetic, the low number of birds treated during the second time interval compared to the first and third intervals, and the lower number of birds treated with a three-day-old solution than with one- or two-day-old solutions.

The return rate of treated and untreated birds was 18.9% and 11.3% for Moustached Warblers and 10.8% and 8.1% for Reed Warblers, respectively (Table 3). For both species, the model that best fit the data was a model with constant survival and recapture probabilities (Table 4). The bootstrap GOF tests were not significant ($P = 0.47$ and $P = 0.91$, respectively). The constant model supports the hypothesis that there were no differences in the survival or recapture probabilities of treated and untreated groups. However, for Moustached Warblers, the second-best model included group effects in survival, but not in recapture, and there was a difference in AIC_c with the constant model of 1.6 units (Table 4). Thus, given the model selection uncertainty, we used model averaging to estimate survival probabilities. Apparent weekly survival was 0.96 ± 0.23 (SE) for the treated group and 0.92 ± 0.25 for the untreated group, and this difference was not significant ($\chi^2_1 = 0.02$, $P = 0.90$; null hypothesis = homogeneous survival rates). The recapture probability for both treated and untreated groups using model averaging was 0.06 ± 0.03.

For Reed Warblers, the second-best model included differences in recapture probabilities between treated and untreated birds, and the difference in AIC_c was > 2 units ($\Delta AIC_c = 2.1$). Indeed, the model suggested lack of difference in survival or recapture probabilities of 2.73 times more support than the second-best model (estimated as the ratio of AIC_c weight). For both treated and untreated groups, weekly survival probability estimated by model averaging was $0.99 \pm 0.08{*}10^{-5}$ and recapture probability was 0.03 ± 0.01.

We obtained body mass changes within 21 days of eight treated and recaptured birds (out of 67 treated individuals) and of 22 untreated and recaptured birds (out of 181 untreated individuals) (Moustached Warbler only). The mean difference in body mass between first capture and recapture was 0.1 ± 0.4 (SD) g for treated birds and 0 ± 0.8 g for untreated birds. This difference was not significant (repeated measures ANCOVA, $F_{1,27} = 0.1$, $P = 0.74$).

DISCUSSION

We obtained samples of stomach contents from 76.7% of birds treated with apomorphine. For all four species combined, the percentage of regurgitating birds was higher than that reported in studies of granivorous birds (range = 43.7 - 71%; see citations in the

Introduction). However, apomorphine has been found to be ineffective with other insectivorous songbirds (Blue and Great tits; Pulido and Díaz 1994, Valera et al. 1997). Díaz (1989) also reported differences in the effectiveness of apomorphine among different families of granivorous passerines, and suggested that effectiveness was influenced by anatomical and physiological differences among different taxa. These differences may include the mechanisms of emesis (e.g., sensitivity of the chemoreceptor trigger zone and its relationship with the vomit center, see Chaney and Kare 1966), structure of the digestive tract (gastric and esophageal muscles), and the relationship between food items size and bird size (e. g., crumbled seeds could be easier to regurgitate than the intact ones) (Díaz 1989). Valera et al. (1997) found that regurgitation was significantly more frequent if birds had ingested soft and easy to crumble seeds. Similarly to Díaz (1989) and Valera et al. (1997), we found differences in effectiveness among species, and the emetic was more effective with Reed Warblers (91.1%). Comparing the effectiveness of apomorphine (as well as its impact on birds) in our study to that of other emetics used in previous studies is difficult because of the wide variety of treated species and procedures and doses adopted, especially for tartar emetic (Diamond et al. 2007 and references therein). Nevertheless, our results and those reported by other investigators who used apomorphine suggest an effectiveness similar to that of tartar emetic (range = 60.5 - 89.8%; see citations in the Introduction) and ipecachuana (68%; Diamond et al. 2007).

No treated birds died before release in our study, and other investigators using apomorphine have reported similar results (Schluter 1988, Díaz 1989, Valera et al.1997, Poulin et al. 2002, Mwangomo et al. 2007). Some investigators using lukewarm water (Ford et al. 1982) and ipecachuana (Diamond et al. 2007) as emetics have also reported no mortality, and others using lukewarm water reported extremely low mortality rates (Brensing

1977, Jenni et al. 1990). In contrast, reported mortality caused by tartar emetic prior to release of treated birds in the wild shows a much wider range (0 – 20%; Tomback 1975, Lederer and Crane 1978, Poulin et al. 1994, Poulin and Lefebvre 1995, Johnson et al. 2002, Poulin et al. 2002, Durães and Marini 2003, Lopes et al. 2005, Zduniak 2005, Carlisle and Holberton 2006, Diamond et al. 2007), although the extremes of this range are reported by studies conducted on small samples (0%, $N = 23$, Tomback 1975; 20%, $N = 10$, Lederer and Crane 1978) or with only one and heavy-size species (0%, Zduniak 2005), being mortality rates of the other studies between 1.5% and 10% (Poulin et al. 1994, Poulin and Lefebvre 1995, Johnson et al. 2002, Poulin et al. 2002, Durães and Marini 2003, Lopes et al. 2005, Carlisle and Holberton 2006, Diamond et al. 2007). Diamond et al. (2007) suggest that the use of non-optimal dosages and particularly stressful procedures could have contributed to an increase in the number of deaths in some cases.

The similar survival and recapture probabilities of treated and untreated birds in our study, plus the similar changes in body mass of treated and untreated groups of Moustached Warblers, suggest that apomorphine had no deleterious post-treatment effects, at least within a few weeks after treatment. Our results are the first assessment of the impact of emetics on birds where survival and recapture probabilities have been distinguished, providing more reliable information than other studies where only return rates (often called “recapture rates” by the authors) are reported. Nevertheless, given our small sample size (especially the small number of recaptured birds) and lack of a real control procedure, additional studies with larger sample sizes are needed before concluding that apomorphine has no post-release effects on treated birds. Using lukewarm water as an emetic, Ford et al. (1982) and Jenni et al. (1990) reported similar return rates for treated and untreated birds and, using ipecachuana, Diamond et al. (2007) reported a significantly higher return rate for treated than untreated birds (34% vs. 22%). Diamond et al. (2007) suggested, however, that this difference could have been due to differences in the species composition of treated and untreated groups. Authors using tartar emetic have reported significantly lower resighting rates for treated than untreated birds (Johnson et al. 2002) and no significant differences in return rates (Poulin et al. 1994, Durães and Marini 2003, Carlisle and Holberton 2006). However, these results should be carefully considered: Durães and Marini (2003) state that they did not follow an experimental approach and that untreated individuals were not randomly chosen, and Poulin et al. (1994) conducted the study on paired plots in which birds did or did not receive the treatment, so that, as noted by Johnson et al. (2002), the effects of the emetic and of study plot on return rate were confounded.

A possible cause of post-release mortality of songbirds treated with emetic is the refusal of feeding. Some researchers using tartar emetic directly observed or found evidences of this negative effect: Zach and Falls (1976) reported that mortality of treated captive Ovenbirds (*Seiurus aurocapillus*) was mainly caused by a refusal to forage for two or three days after treatment. Furthermore, Carlisle and Holberton (2006) found that four of four treated and recaptured birds lost mass, whereas untreated birds were more likely to gain mass (range = 0.08 - 0.41 g). However, other authors using tartar emetic obtained different results: Poulin et al. (1994) treated three birds twice with an interval of 2 – 3 h and found recognizable food items in all six samples, suggesting foraging activity soon after receiving the emetic. Although based on a small sample size (8 treated and 22 untreated birds), our body mass data suggest that birds resumed normal foraging activity after treatment. Similarly, Valera et al. (1997) used apomorphine with captive granivorous songbirds and found that no birds died and all started feeding within 1 h after administering apomorphine.

Considering available information about pre-release mortality of different emetics and our results, tartar emetic can cause a wide range of mortality rates on songbirds, producing no deaths in a few studies, while apomorphine causes no or extremely reduced mortality. The available information about post-release deleterious effects of tartar emetic on free-living birds is contradictory (maybe because of the many variables influencing the effects of the emetic), but studies conducted with captive birds (Zach and Falls 1976, Carlisle and Holberton 2006) suggest that post-treatment effects can be very serious, while our results and treatment of captive birds using apomorphine (Valera et al. 1997) suggest the lack of negative post-treatment effects. Lukewarm water and ipecachuana show a similar impact both before and after treatment than apomorphine, and the currently available information (especially about post-treatment effects) is not detailed enough to determine which of these substances should be considered safest for use with songbirds.

We conclude that apomorphine, as well as ipecachuana and lukewarm water, should be considered useful alternatives to tartar emetic. However, the effects of different emetics on birds can be influenced by many variables such as dosage, bird size, bird species, stress during handling, amount of food in the digestive tracts (see citations in the Introduction) and possibly by many other variables. Anyway, researchers using emetics should take into account the possible biases in representation of different food items in the samples (Zach and Falls 1976, Gavett and Wakeley 1986, Valera et al. 1997). Additional studies with other species and larger samples are needed to better evaluate the possible post-treatment consequences of using apomorphine, especially a rigorous capture-recapture analysis that will allow estimates of survival and recapture probabilities.

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Table 1. Number of birds treated with apomorphine and percent effectiveness of the emetic for each species.

Species	*N* treated	*N* regurgitated	% Effectiveness
Moustached Warbler	67	46	68.7
Reed Warbler	56	51	91.1
Great Reed Warbler	15	10	66.7
Savi's Warbler	12	8	66.7
Total	150	115	76.7

Table 2. Results of the fit of a saturated log linear model[a] including effect of apomorphine (Effect = not regurgitating = 0, regurgitating = 1), time of capture (Time = 0-1.5 h, 1.5-3 h, or > 3 h after opening mist nets), day since preparing the emetic (Day = first, second, or third day), and interactions between factors.

Parameter	Estimation	*Z*	*P*
Effect	-1.946	-2.2	0.026
Time	-1.946	-2.2	0.026
Day	0.963	2.7	0.008
Effect*Day	0.136	0.1	0.89
Time*Day	1.879	2.0	0.047
Effect*Time	1.946	1.3	0.18
Effect*Time*Day	-1.291	-0.8	0.44

[a] Log linear model: Constant + Effect + Time + Day + Effect*Day + Time*Day + Effect*Time + Effect*Time*Day.

Table 3. The number of recaptured Moustached and Reed warblers in treated and untreated groups.

				Recaptured within 21 days		
Species	*N* treated	*N* untreated	*N* total	*N* treated	*N* untreated	*N* total
Moustached Warbler	53	53	106	10 (18.9%)	6 (11.3%)	16 (15.1%)
Reed Warbler	37	37	74	4 (10.8%)	3 (8.1%)	7 (9.5%)
Total	90	90	180	14 (15.6%)	9 (10.0%)	23 (12.8%)

Table 4. The top six CJS models estimating survival (*φ*) and recapture probability (*p*) of Moustached (a) and Reed (b) warblers, in relation to treatment group (g; treated/untreated) and time of capture (t), or with no group nor time effect, i.e., constant (.) survival or recapture probability. For each model, values for corrected Akaike Information Criterion (AICc), the difference between that model and the model with the lowest AICc (Δ AICc), AICc weight, model likelihood, and number of estimable parameters are provided.

a)

Model	AICc	Δ AICc	AICc weight	Model Likelihood	*N* Parameters
φ (.) p (.)	111.911	0.000	0.390	1.000	2
φ (g) p (.)	113.537	1.627	0.173	0.443	3
φ (.) p (g)	113.569	1.658	0.170	0.436	3
φ (.) p (t)	115.542	3.631	0.063	0.163	4
φ (g) p (g)	115.671	3.760	0.059	0.153	4
φ (t) p (.)	116.088	4.177	0.048	0.124	4

b)

Model	AICc	Δ AICc	AICc weight	Model Likelihood	*N* Parameters
φ (.) p (.)	45.606	0.000	0.456	1.000	2
φ (.) p (g)	47.669	2.063	0.163	0.356	3
φ (g) p (.)	47.709	2.104	0.159	0.349	3
φ (.) p (t)	49.799	4.193	0.056	0.123	4
φ (g) p (g)	49.890	4.284	0.054	0.117	4
φ (t) p (.)	49.938	4.332	0.052	0.115	4