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ORIGINAL ARTICLE

Wing marker woes: a case study and meta-analysis of the impacts of wing and patagial tags

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Abstract The marking of individual birds has a long history in ornithology. This inexpensive and simple practice has been used to shed light on migration, behavior, and age-specific survival and recruitment. However, problems associated with markers and tags have often been overlooked. Wing tags have been used for over 40 years on frigatebirds, but their effects on this family of highly aerial seabirds have not been examined. Following higher than expected nest failure of treatment birds in the previous breeding season, we designed a study to test the impact of wing tagging and other standard capture and sampling methods on the nest success of Magnificent Frigatebirds (*Fregata magnificens*). Twelve nests were assigned to each of various band, measure, bleed, wing tag, and control treatments in the 2010/2011 breeding season on Barbuda, West Indies. We modeled nest fates using generalized linear models. Wing tags had a substantial negative effect on pre-fledging nest success, which was 42 % (10/24) for control nests, 39 % (14/36) for all non wing-tagged treatments, and 15 % (7/48) for wing-tagged treatments. We also conducted two meta-analyses, with different effect size calculations, to explore the general impact of wing and patagial tags on all birds. Our log odds ratio model showed a significant effect on survival and hatch and nest success, while our standardized mean difference model dealing largely with outcomes of behavioral, condition, and reproductive parameters (e.g., number of chicks and hatch date) showed no difference between marked and control birds. We consider possible mechanisms by which wing tags might contribute to lower nest success in frigatebirds, and propose that alternative markers be considered carefully before being applied to any species.

Keywords *Fregata magnificens* · Handling effect · Meta-analysis · Mortality · Nest success · Wing tags

Zusammenfassung

Flügelmarkierungen sind möglicherweise problematisch: eine Fallstudie und Metaanalyse der Auswirkungen von Flügelmarkierungen

In der Ornithologie hat die Markierung einzelner Vögel eine lange Tradition. Als preiswerte und einfache Methode dient sie schon seit langem dazu, Erkenntnisse über den Vogelzug, das Verhalten und das Überleben und die Fortpflanzung zu gewinnen. Dabei sind aber Probleme, die aus den solchen Markierungen am Vogel resultierten, oft vernachlässigt worden. Seit mehr als 40 Jahren werden bei Fregattvögeln Flügelmarkierungen eingesetzt, aber deren Auswirkungen auf diese ausgesprochen flugintensiven Vögel wurden nie untersucht. Nachdem wir bei markierten Vögeln nach einer Brutsaison einen schlechteren Bruterfolg als erwartet beobachtet hatten, arbeiteten wir eine Studie aus zur Untersuchung der Auswirkungen von Flügelmarkierungen und anderer Fang- und Markierungsmethoden

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auf den Bruterfolg von Prachtfregattvögeln (*Fregata magnificens*). In der Brutsaison 2010/2011 wurden auf Barbuda, einer Insel der Kleine Antillen, zwölf Nester für je eine von mehreren Markierung- und Messmethoden sowie für Kontrollbehandlungen ausgewählt. Die weitere Entwicklung der einzelnen Nester wurde anhand linearer Modelle modelliert. Danach hatten Flügelmarkierungen einen substantiell negativen Effekt auf den Bruterfolg während der Zeit vor dem Flüggewerden: 42 % (10/24) bei den Kontrollnestern, 39 (14/36) bei allen Behandlungen außer Flügelmarkierung und 15 % (7/48) bei den Nestern mit Flügelmarkierungen. Außerdem führten wir zwei Metaanalysen für unterschiedliche Effektstärkenberechnungen durch, um den generellen Einfluss von Flügelmarkierungen zu untersuchen. Das von uns eingesetzte logarithmische Quotenverhältnis-Modell („log odds ratio model") zeigte einen signifikanten Effekt auf den Überlebens- und Schlüpferfolg, während das standardisierte „mean difference"-Modell, das in erster Linie für Messungen von Verhaltens- und Fortpflanzungsparametern eingesetzt wird, keinen Unterschied zwischen den markierten und den Kontrollvögeln zeigte. Wir denken, dass es möglicherweise Mechanismen gibt, die bei an den Flügeln markierten Fregattvögeln zu einem geringeren Bruterfolg führen, und wir empfehlen, alternative Markierungen bei jeder Vogelart vor einer Anbringung sorgfältig zu prüfen.

Introduction

Simple, inexpensive, field-readable markers are commonly used in studies of migration, behavior, habitat use, population dynamics, and to help form management decisions (Culik et al. 1993). Examples of these markers include colored bands, leg flags, neck bands, and nasal and wing tags. Unfortunately, the problems associated with markers have often been overlooked (Calvo and Furness 1992; Culik et al. 1993). These may include skin abrasion, feather wear, changes in behavior, reduced flying or swimming efficiency, lower reproductive success, increased predation risk, and death (Calvo and Furness 1992; Culik et al. 1993; Zuberogoitia et al. 2012). In a review of the effects of various bird markers, Calvo and Furness (1992) identified a need for careful testing of the effects that marking methods have on the parameters under study, as the use of tags may influence the accuracy of data collected when using them. Here, we test the impact of wing tags as well as other common handling protocols on nest success in Magnificent Frigatebirds (*Fregata magnificens*). To our knowledge, this is the first experimental test of the effects of wing tags on this seabird family (Fregatidae). We initiated this experiment after finding much lower success in nests where at least one adult was handled (5 %, $n = 75$) relative to control nests (no adult handled, 57 %, $n = 81$) in the 2009/2010 breeding season. Our handling protocol used similar methods to previous studies of frigatebirds, including night capture, banding, blood sampling, taking morphological measurements, and marking individuals using alpha-numeric wing tags (e.g., Osorno 1999; Dearborn et al. 2003, 2005; Madsen et al. 2007). Our 2009/2010 data, however, did not allow us to separate effects of tagging from other interventions.

To extend our findings more generally, we also examined the overall evidence for the effects of avian wing markers using meta-analysis, the recommended approach for this type of analysis (Stewart 2010). A quantitative synthesis will clarify how wing-marking techniques affect survival, reproductive, and behavioral parameters.

Methods

Frigatebird nest success

Study site

Barbuda, West Indies (17°37′N, 61°48′W) is a small (160 km^2), low-lying island in the Eastern Caribbean (Online Resource 1). On the northwest edge of the island is the semi-enclosed Codrington Lagoon, where mangroves (primarily *Rhizophora mangle* and *Avicennia germinans*) provide nesting habitat for a Magnificent Frigatebird breeding colony. Diamond's (1973) extrapolation from a partial census of the colony was 2,500 nests in June 1973 (late in the breeding season), and Kushlan (2009) counted 1,743 active nests in March 2009 (mid-season).

Study organism

Frigatebirds are large tropical seabirds that exhibit reversed sexual size dimorphism (females are larger than males) and male ornaments, including a red inflatable gular pouch used in courtship displays; this combination is unique in birds. They rear one highly altricial chick for 12–18 months (Nelson 1975). As in most seabirds, both parents care for the young, but in Magnificent Frigatebirds the male abandons when the chick is 3–4 months old, leaving the female to feed the chick for the remaining long period of parental care (Diamond 1972, 1973; Osorno 1996). Fledging success in frigatebirds is typically low, but probably varies between 15–50 % (Nelson 1975; Diamond and Schreiber 2002). Frigatebirds do not have waterproof plumage, and have small, semipalmate feet, so avoid landing on the surface of the water. They feed by aerial dipping, or more notoriously, by harassing other birds until they disgorge

Table 1 Description of handling treatments assigned to breeding Magnificent Frigatebirds (*Fregata magnificens*) on Barbuda, West Indies, in December 2010

n	Treatment	Description
12 (6 F, 6 M)	Control	Not handled
12 (6 F, 6 M)	Band	Aluminum band applied
12 (7 F, 5 M)	Band + wing tag	Aluminum band and wing tag applied
12 (4 F, 8 M)	Band + bleed	Aluminum band applied and blood sample taken
12 (6 F, 6 M)	Band + bleed + wing tag	Aluminum band and wing tag applied, blood sample taken
12 (5 F, 7 M)	Band + measure	Aluminum band applied and morphological measurements taken
12 (4 F, 8 M)	Band + measure + wing tag	Aluminum band and wing tag applied, morphological measurements taken
12 (8 F, 4 M)	Band + measure + bleed	Aluminum band applied, morphological measurements and blood sample taken
12 (6 F, 6 M)	Band + measure + bleed + wing tag	Aluminum band and wing tag applied, morphological measurements and blood sample taken
Total 108		

Sample size of control nests indicates sex of adults on the nest at the time of nest marking

n sample size, *F* female, *M* male

their stomach contents (Nelson 1975). For their size, frigatebirds have a large wing area and wing span, and extremely low wing loading (mass load per unit area); they take advantage of these features by gliding on thermals at the base of trade wind cumulus clouds to travel great distances in search of food (Pennycuick 1983).

Experimental design

In December 2010, we randomly assigned 12 nests to each of nine treatments [$n = 108$ (56 males, 52 females); Table 1]. Our design tested for main effects of the handling methods used in the previous season: applying a size "7B short" aluminum Bird Banding Lab leg band, taking morphological measurements, bleeding, and attaching wing tags. All nests were uniquely marked with numbered, blue, metal markers approximately 3 cm across with a hole in the top through which snare wire was threaded. The wire was wrapped around a mangrove branch adjacent to the nest. We captured adult Magnificent Frigatebirds on nests by approaching them at night when the moon was set and dazzling them with a headlamp. Eighty-five percent of the nests in this experiment had an egg or chick in December 2010. An adult in breeding condition on a stick nest was considered a nest attempt, since roosting adults not defending nest sites were flightier and more difficult to capture. We processed birds in a small boat in the shallow water adjacent to the colony before returning them to their nests and ensuring that they settled back onto their egg or chick. We did not band the chicks, as their legs are larger in diameter than adults' and problems associated with guano buildup and infection have been reported (Schreiber 1999). We checked nest status in March and May 2011 by walking around the colony to look for nest markers. The final nest check occurred just prior to the fledging of the oldest chicks (it is difficult to determine nest fate after fledging). Therefore, "nest success" was defined as a chick surviving five months post-treatment.

Our wing-tag design was based on those used by others studying Great (*F. minor*) and Magnificent Frigatebirds (Osorno 1999; Dearborn et al. 2003, 2005; Madsen et al. 2007). Made of yellow, 18-oz vinyl-covered nylon, the wing tags were 22.7 cm × 8.5 cm and weighed approximately 8.5 g each (Fig. 1). The number–number–letter combination was hand-painted using black screen ink (System 2 S2 gloss vinyl; Nazdar) and overprint clear (S227; Nazdar) to reduce fading. The tags were placed around the radius and ulna, while facing the underside of the wing, with the central notch on the proximal side (i.e., towards the wrist). The narrowest portion of the tag was passed between two secondary feathers, and each end was rolled up and slipped through the slit in the opposite end to hold the tag in place.

Blood samples were taken by puncturing the brachial vein with a 25-gauge needle and drawing blood up with heparanized microcapillary tubes. We collected up to 120 μL of blood from each bird receiving a "bleed" treatment. Measured birds were weighed using a Pesola spring balance after being placed in a pillowcase, and the weight of the pillowcase was subtracted from the total mass. We measured the right wing from the wrist to the tip of the longest primary, using a butt-ended meter stick, and including the natural curve in the wing (natural chord). Culmen (bill length) was measured using calipers, and semispan (from spine to wing tip) was measured using a meter stick and digital camera.

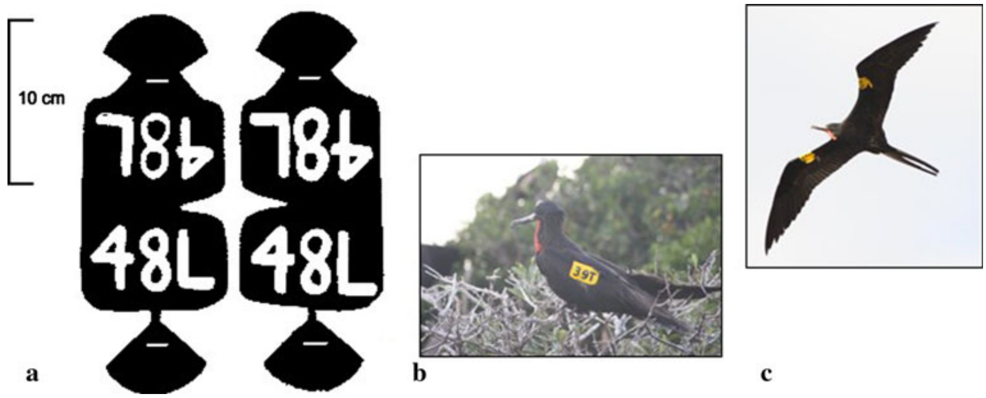

Fig. 1 **a** Wing tags used on adult Magnificent Frigatebirds (*Fregata magnificens*). *Left* tag goes on the bird's left wing. An actual tag is in *yellow* with *black numbers* and *letters*. The narrowest portion of the tag is fitted between two secondary feathers. *White lines* illustrate slits; the tag ends are rolled up and slipped through the slit in the opposite end to secure. Photo of male with wing tags while perched (**b**) and in flight (**c**) (color figure online)

Data analysis

To test the hypothesis that nest success in the treatment groups was not significantly different from control nests, we used a generalized linear model (GLM) with R v.2.8.1 (R Development Core Team 2008) with a binomial error structure (since nest fates were assigned a success/fail status) and a logit link function. Considering the apparent handling effect of the previous season, we considered it biologically relevant to conduct model simplification to better distil the cause(s) of lowered nest success. Therefore, treatments with similar model estimates were pooled one at a time. Each reduced model was compared to the previous model and accepted if not significantly different. Models were ranked using Akaike Information Criterion (AIC).

Our experimental design was not fully factorial, because treating birds (e.g., bleed, measure) requires a handling treatment. In addition, since our goal was specifically to compare each treatment to the control group, we used a priori linear contrasts to test the significance of these comparisons. The "control" and "band" groups had identical nest success (42 %), so we concluded that banding alone was not contributing to nest failures and we pooled these two groups under a single "controls" group against which every other group was compared. Except for this pooling of the first two rows, treatments were coded as they appear in Table 1. Coding the data as presence or absence of each manipulation treatment (i.e., combinations of four treatments) resulted in qualitatively similar results, with no significant interactions among main effects. The coding scheme presented here resulted in seven non-orthogonal contrasts. Since opinion is divided about the need for orthogonality in planned comparisons, we follow the advice of Quinn and Keough (2002), who argue that, if the number of comparisons is small and there is a firm theoretical basis for them, it is more important to examine all the hypotheses than to insist on orthogonality.

Though scientists often focus heavily on the risk of Type I statistical errors ("false positives"), in some applied studies it is important to also consider the risk of Type II statistical errors ("false negatives"), which may have substantial repercussions (Brosi and Biber 2009). Here, aware of the risk of failing to detect a treatment effect if there was one, we adopted a more cautionary approach by setting alpha to 0.10.

Wing-marker meta-analyses

In addition to our experiment, we conducted meta-analyses on the general effect of avian wing markers. Studies using both wrap-around style wing tags, like those used on frigatebirds, and patagial tags, which are placed similarly to wing tags, but require a pin or rod pierced through the patagium to hold them in place, were included.

To obtain wing-marker studies, we first checked all articles in Calvo and Furness' (1992) review for usable studies published prior to 1992. We then searched the Web of Science database for all articles related to the subject using "wing tag*" and "patag* tag*" as key words. Literature cited in relevant papers was also examined. We included experimental and observational studies of both types of wing markers that used "tagged" and "control" (banded or unmarked) treatments. To reduce publication bias, unpublished data were also included: our own "controls" and wing tag treatments presented above, and "control" and "wing tag" nest success from a study on Great Frigatebirds, using the same wing tags we describe (Don Dearborn, 2005, unpublished data). Model results were not qualitatively different when these unpublished data were excluded. In Dearborn's study, unpaired adults in

Table 2 Species considered in the meta-analyses, and classification of order and type of wing marker used

Order	Scientific name	Common name	Marker type	References
Anseriformes	*Oxyura jamaicensis*	Ruddy Duck	Patagial tags	Brua (1998)
Anseriformes	*Somateria mollissima*	Common Eider	Wing tags	Bustness and Erikstad (1990)
Charadriiformes	*Calidris minutilla*	Least Sandpiper	Wing tags	Lank (1979)
Charadriiformes	*Calidris pusilla*	Semipalmaged Sandpiper	Patagial tags	Lank (1979)
Charadriiformes	*Larus delawarensis*	Ring-billed Gull	Wing bands	Southern and Southern (1985), Kinkel (1989)
Charadriiformes	*Scolopax minor*	American Woodcock	Patagial tags	Morgenweck and Marshall (1977)
Charadriiformes	*Sternula antillarum*	Least Tern	Patagial tags	Brubeck et al. (1981)
Charadriiformes	*Tringa semipalmata*	Willet	Wing tags	Howe (1980)
Columbiformes	*Patagioenas fasciata*	Band-tailed Pigeon	Wing tags	Curtis et al. (1983)
Falconiformes	*Falco sparverius*	American Kestrel	Patagial tags	Smallwood and Natale (1998)
Galliformes	*Dendragopus obscurus*	Blue Grouse	Patagial tags	Zwickel (1983)
Galliformes	*Lagopus lagopus scoticus*	Red Grouse	Wing bands	Boag et al. (1975)
Galliformes	*Lagopus lagopus*	Willow Ptarmigan	Wing tags	Hannon et al. (1990)
Gruiformes	*Fulica americana*	American Coot	Patagial tags	Bartelt and Rusch (1980)
Pelecaniformes[a]	*Bubulcus ibis*	Cattle Egret	Wing tags	Maddock and Gearing (1994)
Pelecaniformes[a]	*Egretta garzetta*	Little Egret	Wing tag	Pineau et al. (1992)
Pelecaniformes	*F. magnificens*	Magnificent Frigatebird	Patagial tags	This study
Pelecaniformes	*Fregata minor*	Great Frigatebird	Patagial tags	D. Dearborn, unpub. data (2005)
Psittaciformes	*Calyptorhynchus funereus*	Carnaby's Cockatoo	Wing tags	Saunders (1988)

[a] Classification based on Hedges and Sibley (1994)

breeding plumage were captured and wing-tagged at night in February 2005. Nests of wing-tagged birds scattered throughout the colony and those of birds nesting in three plots (controls) were monitored twice daily to determine incubation success. In spite of extensive research, we failed to discover suitable studies of some large, commonly wing-tagged groups of birds, such as eagles and vultures.

Eighteen published studies on 17 species met our selection criteria and were included in our meta-analyses (Table 2; Online Resource 2). Twelve studies had multiple responses (2–10) that we used to calculate the effect sizes (Online Resource 2). The following data were extracted from the studies: author, publication year, type of tag used (patagial or wing tag), age class of marked birds, study species, and variable(s) measured. When data were presented as means, the treatment and control sample sizes, means, and standard deviations were extracted. In one study the error type was not specified and was assumed to be standard error (Southern and Southern 1985). Standard deviations were calculated as the standard error multiplied by the square root of the sample size if not provided. When data were not presented as means, the number of "successful" and "failed" birds for the tagged and control treatments were used. Birds were coded as "successful", for example, if they returned or were recaptured, or were successful at pairing or hatching eggs, and "failed" if they were depredated or lost chicks.

Meta-analytical procedures

We calculated effect sizes and conducted random-effects meta-analyses on the extracted data using the metafor package (Viechtbauer 2010) for R 2.14.0 (R Development Core Team 2011). Random-effects models were chosen because they incorporate both within- and between-study variability (Hedges and Vevea 1998). We chose to conduct two separate meta-analyses because roughly half of the studies presented data as means and errors, which can be used to calculate a standardized mean difference (SMD) effect size, and the others presented numbers of "successes" and "failures", suitable to calculate a log odds ratio (LOR) effect size. Effect sizes were estimated via weighted least squares, with weight equal to the inverse variance (Viechtbauer 2010). In cases where studies provided data to calculate SMD and LOR effect sizes, we analyzed them separately (e.g., Southern and Southern 1985).

Studies included in the SMD meta-analysis measured condition, reproductive (e.g., number of chicks or fledglings, hatch date), behavioral, and in one case, migratory variables (Online Resource 2). The LOR meta-analysis dealt with survival, hatch success, nest success, and in one case whether tagged birds were successful in establishing a breeding territory. The I^2 statistic, representing the percentage of variability across studies due to heterogeneity rather than chance, is presented for each meta-analysis.

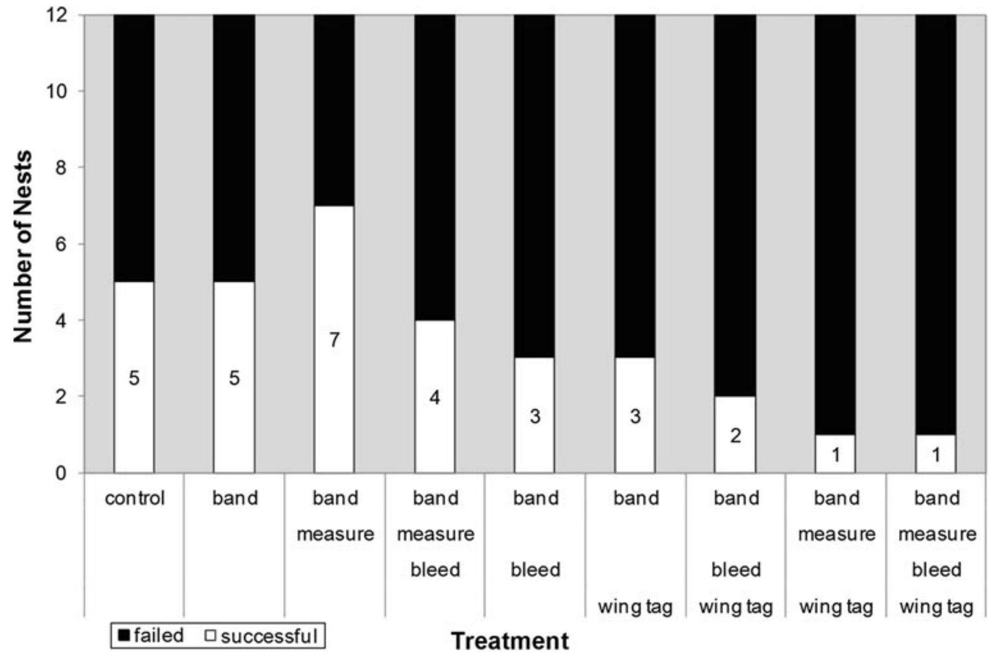

Fig. 2 Nest fates of Magnificent Frigatebirds (*F. magnificens*) breeding on Barbuda, West Indies, were generally lowest for wing tag treatments. Treatments were applied in December 2010 to one adult per nest, and the final nest check occurred in May 2011 prior to fledging

Running a meta-analysis with multiple effect sizes from a single study violates the assumption of the analysis, since data from the same individuals are treated as independent. To test the effect of this violation on the models, we ran 100 iterations of each meta-analysis, randomly selecting one effect size per study in each iteration. These results were not qualitatively different from the meta-analyses on the entire datasets, so for completeness the models and figures presented here include all data. However, the effect of moderator variables (tag type and order) on heterogeneity was explored via a mixed-effects model on one of the random iterations (therefore, using one data point per study). We present funnel plots (scatter plots of the treatment effects against a measure of study size) for each analysis and discuss the possibility of publication bias.

Results

Frigatebird nest success

Behavioral observations

We monitored frigatebirds for up to 15 days after handling, and did not observe any behavioral differences between wing-tagged and control birds. This was consistent with observations from the previous season. We have never observed wing-tagged birds pecking at or pulling their tags, even the morning after capture (*cf* Jackson 1982; Brua 1998). Apparently normal pair bonding behavior, nest exchanges, and copulations occurred. Adults wearing wing tags continued to incubate, brood, lay eggs, and feed young.

Nest fates

Nest success was 42 % for "controls" (birds only handled or banded), 58 % for band + measure, 33 % for band + measure + bleed, 25 % for both band + bleed and band + wing tag treatments, 17 % for band + bleed + wing tag, and 8 % for both band + measure + wing tag and band + measure + bleed + wing tag treatments (Fig. 2). In the initial GLM, the estimate of nest success for each treatment was contrasted with the pooled controls, with an overall AIC score of 131.75 (Table 3a). The two treatments where nest success was significantly lower relative to the controls were "band + measure + bleed + wing tag" and "band + measure + wing tag". The final reduced model (Table 3b) had 3 groups: controls, non wing-tag treatments, and wing-tag treatments, and an AIC score of 126.59. Overall, wing-tag treatments were significantly different from the controls (Table 3). Controls had an overall nest success of 42 %, non wing-tag treatments 39 %, and wing-tag treatments 15 %.

Wing-marker meta-analyses

From the SMD meta-analysis, which included papers with data on means of body condition, reproductive, behavioral, and migratory distance parameters, wing markers had no overall significant effect ($z = 0.549$, $p = 0.583$, mean effect size ± SE = 0.0748 ± 0.1362, $I^2 = 88$ %; Fig. 3).

The LOR meta-analysis model, which included "success" and "fail" data from studies measuring survival and hatch or nest success, showed that wing tags and patagial markers had a significant effect ($z = -5.18$, $p < 0.0001$, mean effect size ± SE = −1.277 ± 0.2466, $I^2 = 69$ %).

Table 3 (a) Full model output of the effects of treatments applied to adult Magnificent Frigatebirds early in the breeding season on nest success; we used a priori contrasts in a generalized linear model analysis, so slope estimates are relative to the controls; two treatments with p values in bold were significantly different from controls at $\alpha = 0.10$.
(b) Reduced model contrasting nest success of wing tag and all non-wing tag treatments; n = sample size

Treatment	Slope estimate	Standard error	z	p	% success
(a)					
Controls ($n = 24$)	−0.34	0.41	−0.81	0.42	42
Band + bleed ($n = 12$)	−0.76	0.78	−0.97	0.33	25
Band + measure + bleed ($n = 12$)	−0.36	0.74	−0.48	0.63	33
Band + measure ($n = 12$)	0.67	0.71	0.94	0.35	58
Band + bleed + wing tag ($n = 12$)	−1.27	0.88	−1.45	0.15	17
Band + measure + bleed + wing tag ($n = 12$)	−2.06	1.12	−1.84	**0.067**	8
Band + measure + wing tag ($n = 12$)	−2.06	1.12	−1.84	**0.067**	8
Band + wing tag ($n = 12$)	−0.76	0.78	−0.97	0.33	25
(b)					
Controls ($n = 24$)	−0.34	0.41	−0.81	0.42	42
Non wing-tag treatments ($n = 36$)	−0.12	0.54	−0.22	0.83	39
Wing-tag treatments ($n = 48$)	−1.43	0.58	−2.46	**0.014**	15

The negative value of the effect size indicates that the probability of success for the treatment (tagged) group is 21.8 % that of the control group, suggesting a negative effect of wing markers on survival and reproduction (Fig. 4).

Comparing the effects of marker types, having patagial ($z = -1.960$, $p = 0.050$, mean effect size ± SE = -1.950 ± 0.995) or wing ($z = -1.993$, $p = 0.046$, mean effect size ± SE = -1.677 ± 0.841) tags had an overall significant negative effect; tagged birds were 12.3 and 15.7 % as successful as controls, respectively. Setting order as a moderator variable, Galliformes were not negatively affected by tags ($z = 2.768$, $p = 0.0056$, mean effect size ± SE = 1.824 ± 0.659), while all other orders were.

A common concern when conducting a meta-analysis is the potential for selective publication of studies showing significance. Funnel plots—scatter plots of the treatment effects estimated from individual data points against a measure of study size—can be useful for diagnosing heterogeneity and publication bias (Sterne et al. 2005). For example, if small studies failing to detect a significant negative effect remain unpublished, then the funnel plot will appear skewed to the right, and the meta-analysis will overestimate the effect (Sterne et al. 2005). In general, there was heterogeneity across data points, for studies with small and large sample sizes (Fig. 5).

Discussion

We suggest that, though wing tags have been used on frigatebirds for over 40 years (Diamond 1975), their use be re-evaluated in light of our experimental evidence. The behavior of adult breeding Magnificent Frigatebirds shortly after wing tagging suggested to us that there was no immediate negative effect of the handling protocol. However, the wing tag treatments had significantly lower nest success relative to controls and to other treatments such as measuring and bleeding. In the original model, our "band + wing tag" treatment had 25 % nest success, which alone may not have raised any alarms had we not tested controls. The nearly three-fold difference in percent nest success of wing-tagged versus control nests raises concerns for us about this marking technique.

Frigatebirds are heavily dependent on soaring flight performance and on agility near the water's surface; their body structure and foraging strategies may cause them to be particularly susceptible to a "wing tag effect". However, our meta-analyses demonstrated that a negative impact of wing tags is not unique to our study. Overall, in studies measuring survival and nest success, wing- and patagial-tagged birds were less successful than controls, while this was not the case in studies measuring condition, behavior, and variables such as number of chicks and hatch date. This suggests that the effects of wing markers on nesting success and mortality are not easily predicted from obvious effects on condition, behavior, or short-term reproductive parameters.

While we did find differences in the effect of tags among orders, we acknowledge small sample sizes and high heterogeneity between studies used in our meta-analyses, and there may be other important variables such as age at marking and study species that we lack the power to test. In this case, publication may be biased by fewer studies showing significant effects of wing markers being published, rather than the reverse, perhaps in part because finding such an effect may invalidate the study. Rigorous tests, particularly of longer-term survival and reproductive parameters (and not only behavior and condition, or other

Reference	Tagged mean (SD)	Control mean (SD)	Standardized Mean Difference [95% CI]
Bartelt & Rusch 1980[1]	−1.9 (8.6)	0.5 (2.7)	−0.72 [−1.03 , −0.42]
Bartelt & Rusch 1980[2]	−4.4 (12.3)	4.2 (5.8)	−1.48 [−2.10 , −0.85]
Brubeck et al. 1981[1]	36.3 (14.1)	28.3 (24.6)	0.40 [−0.45 , 1.26]
Brubeck et al. 1981[2]	1.4 (0.7)	1.8 (0.6)	−0.58 [−1.45 , 0.29]
Southern & Southern 1985[1]	1.22 (7.94)	1.41 (7.16)	−0.02 [−0.34 , 0.29]
Southern & Southern 1985[2]	0.36 (7.94)	0.95 (6.63)	−0.08 [−0.40 , 0.24]
Kinkel 1989[1]	32.3 (4.0)	29.9 (2.5)	0.62 [0.18 , 1.07]
Kinkel 1989[2]	35.1 (6.3)	30.4 (5.0)	0.83 [0.49 , 1.16]
Kinkel 1989[3]	29.8 (3.7)	24.7 (3.1)	1.52 [1.04 , 2.00]
Kinkel 1989[4]	24.7 (3.6)	22.5 (3.6)	0.61 [0.22 , 1.00]
Kinkel 1989[5]	25.5 (4.3)	22.4 (3.9)	0.78 [0.18 , 1.38]
Bustness & Erikstad 1990[1]	28.2 (4.7)	22.9 (3.8)	1.35 [0.85 , 1.86]
Bustness & Erikstad 1990[2]	4.06 (0.8)	4.47 (0.1)	−1.70 [−2.22 , −1.18]
Bustness & Erikstad 1990[3]	99.5 (6.5)	103.4 (8.4)	−0.47 [−0.75 , −0.19]
Hannon et al. 1990[1]	4.9 (4.54)	4.9 (3.73)	0.00 [−0.43 , 0.43]
Pineau et al. 1992[1]	3.43 (0.71)	3.46 (0.83)	−0.04 [−0.96 , 0.88]
Pineau et al. 1992[2]	3.43 (0.71)	3.15 (1.23)	0.25 [−0.67 , 1.17]
McKilligan et al. 1993[1]	300.6 (529.9)	1288 (837.2)	−1.35 [−2.32 , −0.38]
Maddock & Geering 1994[1]	2.11 (0.70)	2.24 (0.77)	−0.17 [−0.43 , 0.08]
Maddock & Geering 1994[2]	2.38 (0.72)	2.30 (0.84)	0.10 [−0.17 , 0.37]
Brua 1998[1]	0.28 (0.60)	1.29 (1.26)	−1.06 [−1.88 , −0.24]
Brua 1998[2]	0.02 (0.08)	0.03 (0.03)	−0.15 [−0.92 , 0.62]
Brua 1998[3]	0.41 (0.48)	0.75 (0.40)	−0.73 [−1.53 , 0.06]
Brua 1998[4]	8.0 (8.0)	3.0 (3.32)	0.74 [−0.05 , 1.53]
Brua 1998[5]	15.0 (8.0)	5.0 (9.9)	1.10 [0.28 , 1.92]
Brua 1998[6]	0.04 (0.06)	0.01 (0.03)	0.61 [−0.36 , 1.59]
Brua 1998[7]	0.02 (0.03)	0.01 (0.03)	0.32 [−0.64 , 1.27]
Brua 1998[8]	0.65 (0.48)	0.77 (0.48)	−0.24 [−1.19 , 0.72]
Brua 1998[9]	6.0 (8.5)	3.0 (9.0)	0.32 [−0.63 , 1.28]
Brua 1998[10]	9.0 (11.3)	1.0 (1.2)	0.98 [−0.03 , 1.98]
Smallwood & Natale 1998[1]	3.00 (1.64)	2.60 (2.31)	0.18 [−0.78 , 1.15]
Smallwood & Natale 1998[2]	3.71 (1.80)	2.60 (2.31)	0.50 [−0.48 , 1.48]
Smallwood & Natale 1998[3]	1.26 (2.01)	0.69 (1.69)	0.29 [−0.41 , 1.00]
Smallwood & Natale 1998[4]	0.33 (0.57)	0.69 (1.69)	−0.22 [−1.47 , 1.04]
RE Model			0.07 [−0.19 , 0.34]

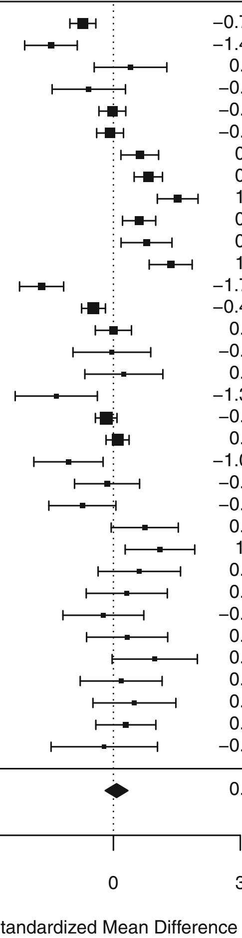

Fig. 3 Forest plot of SMD meta-analysis, showing the results of 34 effect sizes calculated from 11 studies, examining the effects of wing markers on condition, reproduction, behavior, and migratory distance. For each effect size, the standardized mean difference in the marked versus control groups is shown with corresponding 95 % confidence intervals, based on a random-effects (RE) model. Observed effect sizes are drawn proportional to the precision of the estimates. A *diamond* indicates the summary estimate based on the model, with the *outer edges* representing the confidence interval limits. Reference *superscripts* indicate number of within-study effect size calculations, and are the same as in Online Resource 2

short-term measures), are necessary to demonstrate that wing and patagial tags are safe to use for a given species before being widely applied. Experiments testing for a "tag effect" should be designed with sensitivity to Type II error in mind, since failure to detect a small but real effect should be of greatest concern in this instance.

We did not attempt to demonstrate a mechanism by which wing tags reduce nesting success, which is an important step in designing field-readable markers that will not significantly alter the parameters under study or have deleterious effects on survival and reproduction. One possible mechanism leading to lowered nest success is that the color or general appearance of the wing tags caused behavioral changes that affect reproduction, as in Seamans et al. (2010). However, based on our observations of paired birds interacting, tagged bird behavior appeared to mirror that of untagged birds. A second possibility is that the extra mass of two wing tags was great enough to decrease foraging efficiency and mass gain at sea, as in Cory's Shearwaters (*Calonectris diomedea*) wearing 30- and 60-g weights (Passos et al. 2010). However, a pair of wing tags was 1.1 and 1.3 % of female and male mass, respectively; much less than the 3 % limit often used in seabird studies (Phillips et al. 2003). We suggest the likely mechanism causing higher nest failure is that wing tags impair the aerodynamic functioning of the wing. Wing tags likely cause the boundary layer to detach from the wing, which would reduce lift and increase drag, and lower the lift-to-drag ratio; in effect acting like an airbrake on a glider (Pennycuick 2008; C. Pennycuick, personal communication). Aerodynamically, the upper leading edge is the most sensitive part of the wing, which would be disrupted by any

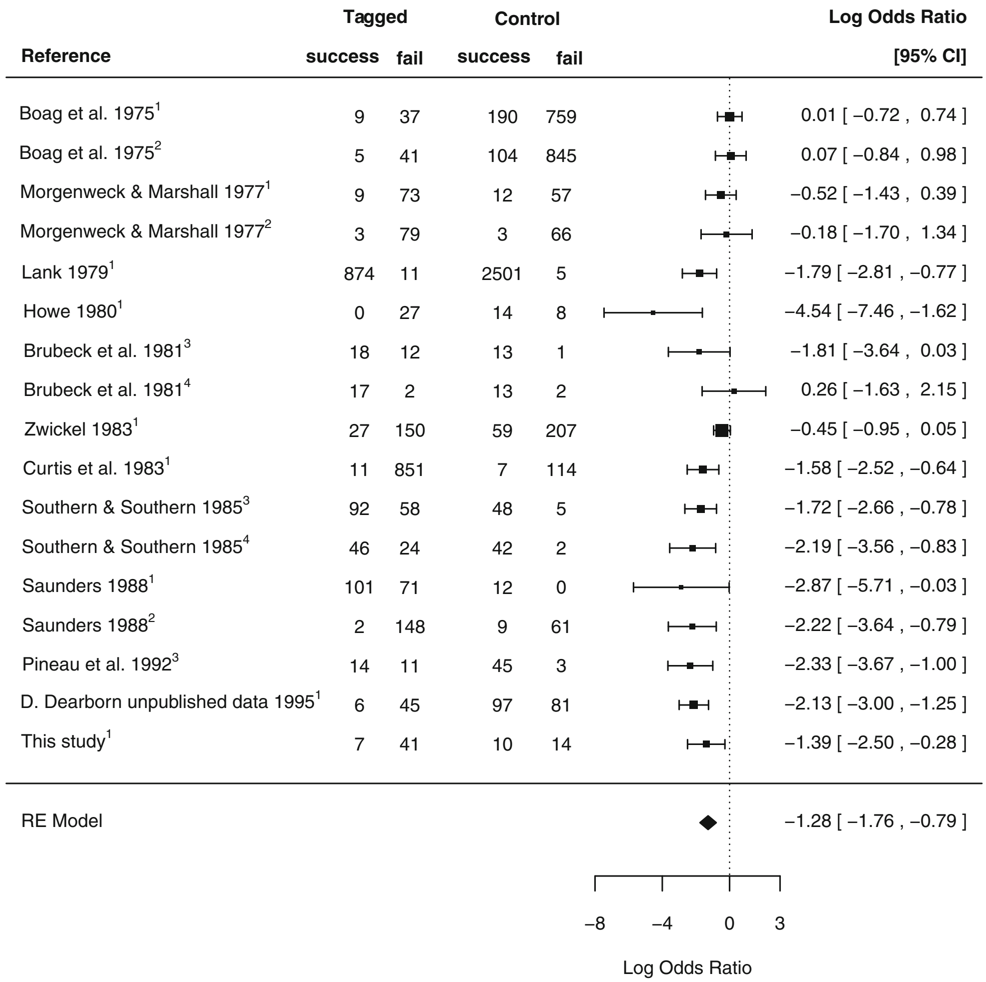

Fig. 4 Forest plot of LOR meta-analysis, showing the results of 17 effect sizes calculated from 12 studies, examining the effects of wing markers on survival and reproduction. For each effect size, the log odds ratio (success versus fail) of the marked versus control groups is shown with corresponding 95 % confidence intervals, based on a random-effects model. Observed effect sizes are drawn proportional to the precision of the estimates, and the summary estimate and confidence intervals of the model are indicated by the *polygon*. Reference *superscripts* indicate number of within-study effect size calculations, and are the same as in Online Resource 2

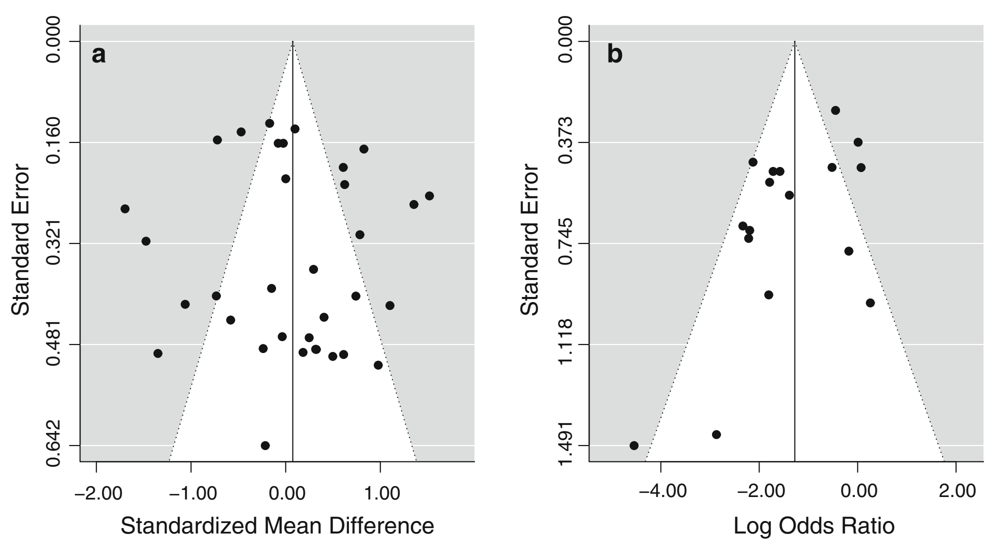

Fig. 5 Funnel plots of the complete data set for **a** the SMD and **b** LOR meta-analyses. Model estimates are indicated by the *vertical lines*, with bounds around the line equal to ± 1.96 × SE

wrap-around style wing tag. The tags may also affect maneuverability, by adding mass (albeit small) at a point on the wing that is subject to large accelerations in flapping flight (Pennycuick 2008). The ends of the wing tags, which occasionally hang down, and the gap sometimes created between the secondary feathers, may also affect flight performance by increasing drag or reducing lift. Wing- and patagial-tag designs, by altering the flow pattern of air over the wing, may increase the energy requirements for flying. With this consideration, other marking strategies should be considered which have less direct impact on a bird's main mode of locomotion.

In light of our evidence of negative effects caused by wing and patagial tags, we recommend against placing field-readable markers on wings, and suggest researchers opt for body-, tail-, or leg-mounted markers, with less aerodynamic consequences. While weight is often taken into consideration with designing markers, it is increasingly clear that reducing drag is also important (e.g., Bowlin et al. 2010; Saraux et al. 2011). For species where colored bands are not practical, one option could be a uniquely marked "fin" made of a thin vertical plastic sheet mounted by attachment to the base of the tail feathers. Another option could be to mount the "fin" on a horizontal base on the bird's back, and hold it in place with loops around the thighs. Such a design would have very little aerodynamic effect (C. Pennycuick, personal communication), but would still need to be rigorously tested for other detrimental effects.

We are not the first to suggest that casual observation of wing-tagged birds' behavior and breeding success is not adequate to determine that tags do not have a significant impact, and that detailed comparison of wing-tagged and untagged birds is necessary to assess the impact of markers on behavior, reproduction, and survival (Howe 1980; Green et al. 2004). The general mechanisms by which we predict wing tags to affect flight performance are not species-specific, and our meta-analysis on survival and reproductive parameters extends our concern regarding the use of wing and patagial tags to other species. The costs to the birds and the reliability of the data obtained may outweigh the benefits of their use.

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References

Bartelt GA, Rusch DH (1980) Comparison of neck bands and patagial tags for marking American Coots. J Wildl Manag 44:236–241

Boag DA, Watson A, Parr R (1975) Patagial streamers as markers for Red Grouse chicks. Bird-Band 46:248

Bowlin MS, Henningsson P, Muijres FT, Vleugels RHE, Liechti F, Hedenström A (2010) The effects of geolocator drag and weight on the flight ranges of small migrants. Methods Ecol Evol 1:398–402

Brosi BJ, Biber EG (2009) Statistical inference, Type II error, and decision making under the US Endangered Species Act. Front Ecol Environ 7:487–494. doi:10.1890/080003

Brua RB (1998) Negative effects of patagial tags on Ruddy Ducks. J Field Ornithol 69:530–535

Brubeck MV, Thompson BC, Slack RD (1981) The effects of trapping, banding, and patagial tagging on the parental behavior of Least Terns in Texas. Colon Waterbirds 4:54–60

Bustness JO, Erikstad KE (1990) Effects of patagial tags on laying date and egg size in Common Eiders. J Wildl Manag 54:216–218

Calvo B, Furness RW (1992) A review of the use and the effects of marks and devices on birds. Ringing Migr 13:129–151

Culik BM, Wilson RP, Bannasch R (1993) Flipper-bands on penguins: what is the cost of a life-long commitment? Mar Ecol Prog Ser 98:209–214

Curtis PD, Braun CE, Ryder RA (1983) Visibility, wear, and effects on survival of Band-tailed Pigeons. J Field Ornithol 54:381–386

Dearborn DC, Anders AD, Schreiber EA, Adams RMM, Mueller UG (2003) Inter-island movements and population differentiation in a pelagic seabird. Mol Ecol 12:2835–2843

Dearborn DC, Anders AD, Williams JB (2005) Courtship display by great frigatebirds, *Fregata minor*: an energetically costly handicap signal? Behav Ecol Sociobiol 58:397–406. doi:10.1007/s00265-005-0933-7

Diamond AW (1972) Sexual dimorphism in breeding cycles and unequal sex ratio in Magnificent Frigate-birds. Ibis 114:395–398

Diamond AW (1973) Notes on the breeding biology and behaviour of the Magnificent Frigatebird. Condor 75:200–209

Diamond AW (1975) Biology and behaviour of frigatebirds *Fregata* spp. on Aldabra Atoll. Ibis 117:302–323

Diamond AW, Schreiber EA (2002) Magnificent Frigatebird (*Fregata magnificens*). In: Poole A (ed) Birds of North America Online. Cornell Lab of Ornithology, Ithaca. doi:10.2173/bna.601

Green AJ, Fuentes C, Vázquez M, Viedma C, Ramón N (2004) Use of wing tags and other methods to mark Marbled Teal (*Marmaronetta angustirostris*) in Spain. Ardeola 51:191–202

Hannon SJ, Jönsson I, Martin K (1990) Patagial tagging of juvenile willow ptarmigan. Wildl Soc Bull 18:116–119

Hedges SB, Sibley CG (1994). Molecules vs. morphology in avian evolution: the case of the ''pelecaniform'' birds. Proc Natl Acad Sci USA 91:9861–9865

Hedges LV, Vevea JL (1998) Fixed and random-effects models in meta-analysis. Psychol Methods 3:486–504

Howe MA (1980) Problems with wing tags: evidence of harm to willets. J Field Ornithol 51:72–73

Jackson JR (1982) Effect of wing tags on renesting interval in Red-winged Blackbirds. J Wildl Manag 46:1077–1079

Kinkel LK (1989) Lasting effects of wing tags on Ring-billed gulls. Auk 106:619–624

Kushlan JA (2009) Status and conservation of the Magnificent Frigatebird (*Fregata magnificens*) on Barbuda, West Indies. J Caribb Ornithol 22:41–43

Lank D (1979) Dispersal and predation rates of wing-tagged semipalmated Sandpipers *Calidris pusilla* and an evaluation of the technique. Wader Study Group Bull 27:41–46

Maddock MN, Gearing DJ (1994) Effect of patagial tags on cattle egrets. Corella 18:1–7

Madsen V, Valkiūnas G, Iezhova TA, Sanchez M, Osorno JL (2007) Testosterone levels and gular pouch coloration in courting Magnificent Frigatebird (*Fregata magnificens*): variation with age-class, visited status and blood parasite infection. Horm Behav 51:156–163

McKilligan NG, Reimer DS, Seton DHC, Davidson DHC, Willows JT (1993) Survival and seasonal movements of the cattle egret in eastern Australia. Emu 93:79–87

Morgenweck RO, Marshall WH (1977) Wing marker for American Woodcock. Bird-Band 48:224–227

Nelson JB (1975) The breeding biology of frigatebirds: a comparative review. Living Bird 14:113–155

Osorno JL (1996) Evolution of breeding behavior in the Magnificent Frigatebird: copulatory pattern and parental investment. PhD dissertation, University of Florida, Gainesville

Osorno JL (1999) Offspring desertion in the Magnificent Frigatebird: are males facing a trade-off between current and future reproduction? J Avian Biol 30:335–341

Passos C, Navarro J, Giudici A, González-Solís J (2010) Effects of extra mass on the pelagic behavior of a seabird. Auk 127:100–107

Pennycuick CJ (1983) Thermal soaring compared in three dissimilar tropical bird species, *Fregata magnificens, Pelecanus occidentalis* and *Coragyps atratus*. J Exp Biol 102:307–325

Pennycuick CJ (2008) Modelling the flying bird. Academic, Amsterdam

Phillips RA, Xavier JC, Croxall JP (2003) Effects of satellite transmitters on albatrosses and petrels. Auk 120:1082–1090

Pineau O, Hafner H, Kayser Y (1992) Influence of capture and wing tagging on the little egret (*Egretta garzetta*) during the breeding season. Rev Ecol (Terre Vie) 47:199–204

Quinn G, Keough M (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org

R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org

Saraux C, Le Bohec C, Durant JM, Viblanc VA, Gauthier-Clerc M, Beaune D, Park Y, Yoccoz NG, Stenseth NC, Le Maho Y (2011) Reliability of flipper-banded penguins as indicators of climate change. Nature 469:203–206

Saunders DA (1988) Patagial tags: do benefits outweigh risks to the animal? Aust Wildl Res 15:565–569

Schreiber EA (1999) Problems encountered when banding frigatebirds and boobies. Waterbirds 22:310–313

Seamans TW, Beckerman S, Hartmann J, Rader JA, Blackwell BF (2010) Reporting difference for colored patagial tags on Ring-billed gulls. J Wildl Manag 74:1926–1930. doi:10.2193/2009-304

Smallwood JA, Natale C (1998) The effect of patagial tags on breeding success in American Kestrels. North Am Bird Bander 23:73–78

Southern LK, Southern WE (1985) Some effects of wing tags on breeding rRing-billed gulls. Auk 102:38–42

Sterne JAC, Becker BJ, Egger M (2005) The funnel plot. In: Rothstein HR, Sutton AJ, Borenstein M (eds) Publication bias in meta-analysis: prevention, assessment, and adjustments. Wiley, Chichester

Stewart G (2010) Meta-analysis in applied ecology. Biol Lett 6:78–81

Viechtbauer W (2010) Conducting meta-analysis in R with the metafor package. J Stat Soft, 36:1–48. URL http://www.jstatsoft.org/v36/i03

Zuberogoitia I, Arroyo B, O'Donoghue B, Zabala J, Martínez JE, Murphy SG (2012) Standing out from the crowd: are patagial wing tags a potential predator attraction for harriers (*Circus* spp.)? J Ornithol. doi:10.1007/s10336-012-0842-2

Zwickel FC (1983) Factors affecting the return of young blue grouse to breeding range. Can J Zool 61:1128–1132