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TECHNICAL REPORT

The potential costs of flipper-bands to penguins

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Summary

1. The published literature on the effects of flipper-bands on penguin ecology is reviewed. Six published studies show the following.

2. In Adélie Penguins *Pygoscelis adeliae*, flipper-bands directly damaged flippers, increased swimming costs by 24%, decreased survival in the first year after banding by 28%, and may have accelerated decline of a dwindling colony by 3%.

3. Adult return rates to colonies among flipper-banded Adélie, Chinstrap *P. antarctica* and Gentoo *P. papua* Penguins decreased by 8%, 12% and 25%, respectively, between single- and double-banded penguins. Juvenile return rates among Gentoo Penguins were reduced by 10·5%. Return rates to the colony among double-banded King Penguins *Aptenodytes patagonicus* were 31·3% and 6·7% lower than among single-banded birds in the first and second years after banding, respectively, and single flipper-banded birds showed annual survival rates 21·1% lower than those of birds fitted with subcutaneous transponders.

4. Among Royal Penguins *Eudyptes schlegeli*, there were no differences between chick growth, adult over-winter survival and fledging success between flipper-banded birds and birds fitted with transponders.

5. Adélie Penguin adult annual survival rates were lower among flipper-banded birds than among unbanded birds.

6. On the basis of dive profiles for Adélie Penguins, it is estimated that increased swimming costs of 5% reduce prey contact time by 10%, and of 24% reduce prey contact time by 48%. These estimated 'knock-on' or cumulative costs coupled with the survival and breeding costs shown by the majority of published field studies suggest that data collected on some flipper-banded populations are biased.

7. The advantages and disadvantages of an alternative long-term marking technique, subcutaneously implanted passively interrogated transponder tags, are discussed. Research projects currently testing transponders and flipper-bands worldwide are listed.

Key-words: Conservation, energetics, foraging costs

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Introduction

Flipper-bands have been used by ecologists to mark penguins for more than 50 years (Sladen 1952), and their use has been increasingly debated by penguin researchers at forums such as the Third and Fourth International Penguin Conferences and workshops hosted by the National Research Foundation of the United States of America, and the Scientific Committee on Antarctic Research (Fraser & Trivelpiece 1994; Anonymous 1997; Fraser 1997). The bands comprise flat metal strips moulded to embrace loosely the axillary part of the flipper, and each is stamped with a unique number that is readable at a distance. We consider the time right for a re-evaluation of the use of these bands because technological advances in the past decade have altered field studies of penguin biology in two ways. First, as our understanding of penguin life at sea (i.e. hydrodynamics, swimming costs, dive profiles and time partitioning during and between dives) has improved, so too has our understanding of the costs borne by penguins wearing flipper-bands (Culik, Wilson & Bannasch 1993; Bannasch 1994; Bannasch, Wilson & Culik 1994). Second, new transponder technology now permits individual birds to be marked using small transponders (e.g. 23 mm × 3 mm for the commonly used Tiris™ transponders, Texas Instruments, Dallas, Texas), which may be injected subcutaneously (Kerry, Clarke & Else 1993; LeMaho *et al*. 1993). A

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drawback of this technique is that marked and marked birds are indistinguishable by eye to field biologists. However, transponders do not alter birds' hydrodynamic drag and therefore may be a desirable alternative marking technique if their invisibility can be accommodated.

Published papers on penguin flipper-bands may be divided into two main categories. First, studies from the late 1950s until the early 1980s focused on the design of bands with an eye to maximizing band lifespan. Second, fieldwork by Ainley, LeResche & Sladen (1983) and subsequent authors has explored the effects of flipper-bands on adult and juvenile survival, breeding success and energetics. Consequently, reviews of flipper-band effects include the proceedings of two recent international workshops which concluded that flipper-bands should no longer be recommended as the method of choice in penguin studies, and that alternative marking techniques should be sought and tested. Stonehouse (1999) highlighted many of the detrimental effects of bands on penguin individuals and populations, concluding with a call for improved band materials rather than for the complete replacement of this marking method with transponder use.

Here we summarize the literature on the effects of penguin flipper-bands on the energetics and life-history characteristics of their wearers. Existing field data are used to estimate the influence of band-induced increased energy costs on penguin dive profiles. Because Cooper & Morant (1981) and Stonehouse (1999) have thoroughly reviewed the changing design of flipper-bands, we do not duplicate their emphasis here, but list current studies investigating flipper-band design. We review three field studies testing flipper-band effects that were not yet published when Stonehouse's (1999) review went to press (Trivelpiece & Trivelpiece 1994; Clarke & Kerry 1998; Froget *et al*. 1998). We discuss the advantages and disadvantages of transponders, albeit briefly because this technique is reviewed elsewhere (Behlert & Willms 1992; Kerry *et al*. 1993; Clarke & Kerry 1998; Dann 2000).

The final factor that precipitated the present review is a recent large-scale banding operation of 20 000 African Penguins (*Spheniscus demersus* Linnaeus) in South Africa following the birds' rehabilitation after an oil spill near the third-largest breeding colony of this species. Flipper-banding of 11% of the world's population of a species listed as vulnerable by the IUCN and the Red Data Book for South Africa, Lesotho and Swaziland (Crawford 2000) calls for a re-examination of this marking technique and a decision about future choices for permanently identifying birds used in ecological studies.

Flipper-band design

Before publication of the results of a long-term study on Adélie Penguins *Pygoscelis adeliae* Hombron & Jacquinot (Ainley *et al*. 1983), debate about band design focused on researcher convenience rather than cost to the marked birds. For example, Sladen & LeResche (1970) considered the 'ideal band' to be 'one which will outlive the bird'. The material from which bands were made changed from the initially used aluminium (Sladen & Penney 1960) to more durable stainless steel (Cooper & Morant 1981). Altering the material influences the lifespan of the flipper-band rather than its effects on the bird. From a hydrodynamic perspective, band material is less important than whether or not the band has an overlapping locking device (Sladen & Penney 1960) or a flattened safety fastener (Sallaberry & Valencia 1985). The original aluminium bands used by Sladen and coworkers were fitted to birds in the field by crimping the band ends, leaving a join that was not flush with the band. This design resulted in considerable wounding of pygoscelid penguins (Adélie *Pygoscelis adeliae*, Chinstrap *P. antarctica* Forster and Gentoo *P. papua* Forster Penguins). This type of band is no longer in use (Sallaberry & Valencia 1985).

Current bands are all made from stainless steel. The studies that we review employed both aluminium (Ainley *et al*. 1983) and stainless steel bands (all other studies). When properly applied, modern bands of the correct size are preshaped and closed with special pliers so that the band ends abut to produce a flush fit. Stonehouse (1999) suggested that alternative materials such as plastic should be investigated. Plastic bands fit the flipper snugly and therefore may not influence hydrodynamics to the same extent as do loose stainless steel flipper-bands, yet they expand during moult to reduce or prevent the potentially fatal flipper damage that an overly tight non-elastic band may induce. Plastic flipper-bands are being tested on captive penguins at the Bristol Zoo (Barham 1999). Field testing of these bands on African Penguins at Robben Island, South Africa, commenced in March 2001 with comparisons of breeding success and other life-history parameters between unbanded birds and birds wearing either plastic or stainless steel bands (L. G. Underhill, personal communication).

A study investigating flipper-band design is currently being conducted at Punta Tombo, Argentina as part of a long-term study of Magellanic Penguins *Spheniscus magellanicus* Forster (P. D. Boersma, personal communication), but no results were available at the time of this review.

Flipper-band effects on penguin life history

Fieldwork over the past 17 years has sought to assess the effects of flipper-bands on penguins by examination of individuals (Sallaberry & Valencia 1985), by studies of breeding biology, population size and annual survival (Ainley *et al*. 1983; Trivelpiece & Trivelpiece 1994; Clarke & Kerry 1998; Froget *et al*. 1998), and by controlled studies of swimming costs among banded birds (Culik *et al*. 1993). Taken together, these studies are the most important source of data which should help answer the

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questions: do flipper-bands carry an acceptable cost to their wearers, and to what extent might data collected from flipper-banded penguins be influenced by the presence of the bands themselves?

During the 1960s, Ainley *et al*. (1983) banded 364 Adélie Penguins aged from 4 to 7 years at Cape Crozier in the Antarctic as part of a long-term study of the biology of this species. The bands used were aluminium, 10 mm wide with flush-fitting edges (Sladen & Penney 1960). Newly banded birds showed a 28% lower survival rate in the first year following banding than they did in the second, third and fourth years after banding. Ainley *et al*. (1983) suggested that this initially enhanced mortality was partly attributable to flipper injuries caused by swelling during moult, and also referred to the possibility of an unknown band-induced mortality affecting survivorship in older birds. These authors reported that Adélie Penguin colony size was decreasing at Cape Crozier during the 1960s, with the banded population declining 3% more rapidly than the unbanded one.

Culik *et al*. (1993) measured oxygen consumption using flow-through respirometry in Adélie Penguins swimming to and fro in an artificial swim tunnel on Ardley Island in the South Shetland Islands, Antarctica. Flipper-banded birds swam slightly but not significantly slower than did unbanded birds. The cost of transport (energy required for swimming at all speeds measured between 1·4 and 2·2 m s^{-1}) was measured for seven birds swimming with and without flipper-bands, and was found to be 24% higher when the birds were wearing bands. Such increases in the energetic cost of swimming likely have non-linear knock-on effects on foraging efficiency. Penguins dive aerobically (Butler & Jones 1997). Increases in swim costs reduce the aerobic dive limit (ADL *sensu* Butler & Jones 1997) and thus the amount of time that penguins can remain underwater exploiting prey. The magnitude of the effects of increased oxygen consumption and reduced ADL may be estimated by a simple exercise. The average length of an Adélie Penguin feeding dive to 75 m depth is 2 min (Ropert-Coudert *et al*. 2001; Wilson *et al*., in press), of which 1 min is spent descending to and ascending from the depth at which the prey are found, and 1 min is spent pursuing prey. An increase of only 5% in oxygen consumption would reduce ADL by the same factor, reducing the total length of a 2-min dive by 6 s, but the 'commuting' time taken to reach prey would remain the same. The penguin would thus have 120 – 6 – 60 s left for foraging, i.e. 54 s, rather than 60 s. This amounts to a 10% reduction in available foraging time, doubling the apparent cost of 5%. Similarly, for the same dive profile a theoretical increased swimming cost of 24% in swimming costs (the observed increase) would reduce foraging time by 28·8 s, nearly 50%. This effect might be ameliorated over time as birds become accustomed to flipper-bands (Hindell, Lea & Hull 1996). However, even small reductions in foraging efficiency might be felt by birds in times of prey shortage, leading Clarke & Kerry (1998) to speculate that flipper-band effects may have accounted for the apparently high mortality rate they observed among banded Adélie Penguins in the winter of 1995.

Penguin prey is encountered in patches (Wilson 1995), a fact critical for foraging energetics. Prey patches are encountered after a specific time spent searching (Wilson & Wilson 1995) and the prey in each patch can only be exploited during a specific number of dives (Wilson & Wilson 1990, 1995) during each of which time underwater is limited by the rate of energy expenditure. Birds with a 24% increase in swim costs during patch searching have to try to correct for this increased cost by greater ingestion within patches even though they incur a decrease of 24% in foraging time in the patch, leading to an effective decrease in foraging efficiency that is probably double 24% (see above).

Finally, on the basis of data on penguin swim energetics and hydrodynamics (Bannasch *et al*. 1994), Culik *et al*. (1993) concluded that attaching a loosely fitting band onto 'a highly specialized propelling structure such as a penguin's flipper compromises many of its capabilities.' Aerobic dive limit may be still further reduced by the high swim speeds associated with prey capture (e.g. Wilson & Wilson 1995), because energy expenditure increases non-linearly with drag (including the drag caused by the band) which itself increases as a function of the cube of the swim speed (Boyd, Reid & Bevan 1995; Culik *et al*. 1996; Bethge *et al*. 1997). Small impairments of function might lead to large differences in survival by influencing birds' abilities to twist and turn in pursuit of prey, thereby decreasing foraging success in young penguins and in birds naive to the presence of a flipper-band.

The energy costs associated with flipper-bands could be conclusively assessed by comparing field metabolic rates between transponded and flipper-banded birds using doubly labelled water (e.g. Nagy, Wilson & Siegfried 1984), but the experimental variability associated with this technique may mask small increases in foraging costs that are nonetheless significant to the birds. Such a comparison has not yet been published for any species.

Trivelpiece & Trivelpiece (1994) compared mortality and return rates between groups of single- and double-banded Adélie, Gentoo and Chinstrap Penguins. Single-banded birds wore a band on one flipper only, whereas double-banded birds had a band on each flipper. For all three species, return rates among double-banded birds were lower than those among single-banded birds being 31% *vs* 39%, 31% *vs* 56% and 32% *vs* 44% for double- *vs* single-banded Adélie, Gentoo and Chinstrap Penguins, respectively. Moreover, these authors inferred survival of Gentoo Penguin chicks from return rates of chicks to the colony after their first year at sea. Whereas 84 of 800 single-banded birds returned to the colony (11%), only one of 200 double-banded birds (0·5%) returned after the same time period. These authors are currently comparing mortality of birds fitted with subcutaneous transponders with that among flipper-banded birds (see below).

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Hindell *et al.* (1996) fitted 158 Royal Penguins *Eudyptes schlegeli* Finch on Macquarie Island with transponders (Tiris™ Systems), and fitted half of this group (78 birds) with flipper-bands. They compared adult over-winter survival, growth of chicks with banded parents and fledging success between the banded and unbanded groups, and found no differences. They concluded that flipper-bands have no adverse effects on Royal Penguins, with the caveat that their study encompassed one year only and therefore did not take cumulative effects (*sensu* Froget *et al.* 1998; see below) into account. They speculated that Royal Penguin adults may have sufficient energy reserves to buffer the effects of flipper-bands for one year.

As part of a long-term study of King Penguins *Aptenodytes patagonicus* Miller at the Crozet Archipelago, Froget *et al.* (1998) fitted birds with either single ($n = 193$) or double flipper-bands ($n = 190$), and compared numbers of birds in these groups returning to the colony with data for birds in an adjacent area of the same colony which were wearing only transponders (Tiris™ Systems, see below). Return rates during the first and second years after banding were lower among double-banded than among single-banded birds (45·2% and 68·6% for the first and second years among double-banded birds, compared to corresponding figures of 75·6% and 75·3% for single-banded birds). These authors estimated annual survivorship among unbanded transponded birds of this species to be 96·5%, suggesting that banding reduces survival, particularly in the first year after banding. Flipper-banded birds showed higher hatching success, but lower fledging success compared with transponded birds, although the latter difference might have resulted from the position of birds in the colony. Despite their low breeding success in the first year of the study, the majority (67·5%) of flipper-banded (double and single) birds laid late (in January) the following year. This contrasts with the usual pattern of behaviour observed for this species, in which birds that fail to fledge chicks in a given year lay earlier the following year. The authors suggested that the low fledging success that they observed may have been because chicks with banded parents were underfed during winter. The authors concluded that flipper-banding has a detrimental effect on both survival and reproductive success in King Penguins, and that alternative marking methods should be sought.

Clarke & Kerry (1998) compared return rates of adult Adélie Penguins to the colony in three cohorts of birds marked during the summers of 1991–92, 1992–93 and 1993–94. Approximately half the birds (total $n = 149$) were marked with both flipper-bands and subcutaneous transponders, and half ($n = 184$) were fitted only with transponders. Between 1992 and 1997, annual return rates for each cohort were consistently but not significantly lower among flipper-banded birds, with differences between the two experimental groups (expressed as the annual percentage return for the transponder-only group minus that for the transponder plus flipper-band group) ranging from –2% to 26% (Table 1). Out of 12 such comparisons, in one case the return rate of banded birds was higher than that among unbanded birds, in one case the return rates were equal, and in 10 cases banded birds showed lower return rates than did unbanded birds. The greatest differences between experimental groups (10%, 26% and 14% for the three cohorts, respectively) were for the period spanning the summer of 1995, during which there was a prey shortage. Clarke & Kerry (1998) conclude by recommending the use of subcutaneously implanted transponders, with a number of caveats, which are outlined below. They suggest that, when prey is scarce, the extra energy required to swim with a flipper-band may compromise the survival of banded birds. They also emphasize the damage caused by monel bands that open after some time on the bird, even if closed properly on application. Birds probably manipulate bands with their bills, leading in two cases to severe flipper damage by partially opened bands, and another where a bird's bill became trapped in the band (Clarke & Kerry 1998; K. Kerry, personal communication).

Consideration of the suitability of flipper-bands on a study-by-study basis must take cognisance of the fact that as foraging behaviour differs among penguin species and among breeding sites, so too may flipper-band effects (Anonymous 1997; Fraser 1997). To date, however, no clear trends emerge from the published data. Foraging radius influences relative costs of prey capture, and so may mitigate or exaggerate any effects of flipper-bands. If flipper-bands increase swimming costs, as they appear to do, the more swimming a penguin has to do to obtain a given amount of prey, the greater the potential impact of flipper-bands. Despite this, although Gentoo Penguins have more restricted foraging ranges than other pygoscelids (Wilson 1995), this species shows a more pronounced band-induced decrease in return rate to the breeding colony (Trivelpiece & Trivelpiece 1994). Speculation about interspecific differences in flipper-band effects is therefore premature on the basis of the existing literature.

Of the above six published studies, four found that flipper-bands carry substantial life-history and energetic costs to penguins, one found no significant adverse effects (Hindell *et al.* 1996), and one (Clarke & Kerry 1998) found statistically insignificant effects that the authors nonetheless suggested had biological significance, and that prove significant when we applied a different statistical test to the published data (Table 1). A seventh study in preparation for publication shows significantly reduced adult survival in flipper-banded Little Penguins *Eudyptula minor* Forster (P. Dann, personal communication, see below). The balance of evidence suggests therefore that use of flipper-bands to mark penguins is probably detrimental to the birds' survival, particularly among juveniles and during times of prey shortage.

Our conclusion has two important corollaries: (i) consideration of the scientific validity of data collected using flipper-banded populations and (ii) the moral obligation that we have to minimize stress to the animals

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Table 1. Summary of the effects of flipper-bands on penguin ecology. All values are percentages of total population marked or, in the case of swimming costs, of values for unbanded birds. Sample sizes are given in parentheses after measurements, except where no sample sizes were reported in the original study

Parameter	Penguin species	Birds marked with: Transponder (*n*)	Single band (*n*)	Double band (*n*)	Significant difference	Reference
Juvenile return rate to colony	Gentoo		11% (800)	0·5% (200)	10·5%	Trivelpiece & Trivelpiece (1994)
Adult return rate to colony	Adélie		39%	31%	8%	Trivelpiece & Trivelpiece (1994)
	Gentoo		56%	31%	25%	Trivelpiece & Trivelpiece (1994)
	Chinstrap		44%	32%	12%	Trivelpiece & Trivelpiece (1994)
Annual adult return rate to colony	Adélie	184	149		−2 to 26%*	Clarke & Kerry (1998)
Return rate to colony (1st year after banding)	King		76·5% (193)	45·2% (190)	31·3%	Froget *et al.* (1998)
Return rate to colony (2nd year after banding)	King		75·3% (193)	68·6% (190)	6·7%	Froget *et al.* (1998)
Annual survival	King	96·5% (600)	75·4% (600)		21·1%	Froget *et al.* (1998)
Annual survival in first banded year *vs* other groups	Adélie		−28% (364)		28%	Ainley *et al.* (1983)
Over-winter survival	Royal	76% (158)	67% (78)		–	Hindell *et al.* (1996)
Cost of swimming	Adélie		+24% (7)		24%	Culik *et al.* (1993)

*Difference not statistically significant (χ^2 with 1 df), 10 out of 12 comparisons showed lower return rates among banded birds compared to unbanded. Mann–Whitney *U*-test comparing annual returns as percentages shows significant difference between banded and unbanded birds ($P < 0{\cdot}033$).

we study. However, most pertinent is the extent to which we allow manipulated animals to depart from demonstrable norms. Determination of norms with regard to penguins is problematic since any form of marking appears to effect departures from the norm (e.g. Wilson & Culik 1992). However, the use of techniques such as double banding highlights potential problems: here the difference between two bands and one may be considered to the equivalent of the difference between one band and none. With this proviso in mind, what, then, is an acceptable departure from the norm? A rule of thumb for devices on birds is that they should not exceed 5% of the mass of the carrier (Calvo & Furness 1992), this being related to loads and flight capabilities (Obrecht, Pennycuick & Fuller 1988; Wilson, Ryan & Wilson 1989). The problem of mass, however, may be essentially irrelevant in penguins where streamlining is far more critical and loads carried for chicks comprise up to 30% of the body mass. If, nonetheless, we opt for a blanket rule of 5% irrespective of the parameter, it is clear that the effect of bands on penguins induce aberrant effects that exceed this on most counts (Table 1), despite their negligible mass. Over and above this, we feel it unacceptable that any system induces a differential mortality for the effective wearing period, as flipper-bands on penguins appear to do.

Finally, a study of flipper-band effects on the African Penguin *Spheniscus demersus* is currently under way. Approximately 20 000 adult and juvenile individuals of this species were flipper-banded and released following their rehabilitation after an oil spill in June 2000. This represents 11% of the world's population of the species, which was estimated at 179 000 birds in the early 1990s (Crawford *et al*. 2000). Superimposed upon the mortality and lowered future breeding success imposed by the oiling of the birds (Briggs, Yoshida & Gershwin 1996), flipper-band effects on this population would be considerable should the species follow the same pattern as the six other penguin species for which data are reviewed here. Long-term life history characteristics will henceforth be assessed in the Robben Island colony of African Penguins that was worst affected by the above spill (e.g. Crawford *et al*. 2000). Total sightings of banded African Penguins in the 5 years since a previous oil spill (the Apollo Sea spill) in 1994 have been 73% of a total of 4076 birds flipper-banded in that spill (Underhill *et al*. 2000), but this is a cumulative total rather than an annual survivorship value. In the year between 1 August 1998 and 1 August 1999, 28% of the original cohort of banded birds were sighted, but sightings are not comparable to dedicated surveys assessing return rates to colonies. Annual adult survival of this species is estimated to be 90% (Crawford, Shannon & Whittington 1999).

Workshop reports

In July 1993, the US National Science Foundation funded a workshop on Researcher–Seabird Interactions in

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Monticello, Minnesota. The workshop report was published by the US Office of Polar Programs (Fraser & Trivelpiece 1994). Consensus statements on banding and marking techniques in this report recommended the development of methods alternative to flipper-bands for permanent individual marking of penguins. One alternative suggested was transponders, and an urgent call was made for the assessment of their efficacy and effects on study populations. The report also recommended that significant design improvements to flipper-bands might be accomplished through the use of alternative materials, but cautioned that bands made of new materials should be subjected to thorough testing for drag and other effects.

In July–August 1996, a meeting of the Bird Biology Subcommittee of the Scientific Committee on Antarctic Research (SCAR) was held in Cambridge, UK. A workshop on penguin marking techniques was held during this meeting (Anonymous 1997; Fraser 1997). The participants agreed that multiyear marking techniques were necessary, but advised that 'flipper-bands should no longer be recommended as the method of choice' for this purpose (Fraser 1997). A 'highly cautionary approach to the use of flipper-bands' was advocated (Anonymous 1997), probable interspecific differences in band effects were highlighted, and the desirability of exploring alternative long-term marking techniques was expressed.

Alternative marking technology

The use of subcutaneously implanted transponders was pioneered in January 1991 at Possession Island in the Crozet Archipelago by LeMaho *et al*. (1993), who studied King Penguins, and in November 1991 by Kerry *et al*. (1993), who studied Adélie Penguins near Mawson Station in the Antarctic. Both groups of researchers used a system manufactured by Tiris™ Instruments. Transponder tags (24–32 mm × 3 mm for Adélie Penguins, 30 mm × 3 mm, 0·8 g for King Penguins) were surgically implanted under the birds' skin. Identification takes place at a distance of 0·3–0·7 m from a detector as birds walk over a bridge. Both research groups considered that this approach has great potential as a marking and logging system for future studies. Birds at nests can be readily scanned by researchers using hand-held transponder readers moved to within 0·3–0·7 m of the bird. Commuting paths to and from colonies are often manipulated by researchers so that all birds entering and leaving the colony are forced to walk across a weigh-bridge combined with a tag reader. This is usually accomplished by fencing whole colonies or sections thereof, a practice that has been successfully applied with Adélie Penguins, which show little difference in breeding success inside and outside fenced areas (K. Kerry, personal communication). Fences may cause disturbance to the birds, but this is minimized if researchers locate fence lines with care to ensure that natural pathways are accommodated. Attention should be paid to enhanced predation risks incurred by birds unable to move freely in fenced sections of colonies (K. Kerry, personal communication).

The advantages of the transponder system are that it does not carry the high energy cost to the birds that stainless steel flipper-bands do (see above), and that it can automatically log the movements and body masses of large numbers of birds round the clock. The disadvantages of the system include transponder failure after a period of 5 years or more, or failure of readers to register birds. Transponder use is considerably less convenient for researchers than is the use of flipper-bands, because birds marked with such small subcutaneous devices cannot be identified by sight at a distance on land. Clarke & Kerry (1998) recorded that a transponder recovered from one bird had developed a slimy biofilm containing potentially pathogenic bacteria. Such effects presumably arise from bacteria entering the wound at the time of implantation, and could well result in long-term infections in marked birds. Such consequences can be minimised by antiseptic implantation procedures. Transponders may be lost through the entry wound if inserted in an anterior direction. Finally, transponders, particularly larger ones, may migrate away from implantation sites and could cause damage (Clarke & Kerry 1998). For this reason, these authors recommend that sites far from vital organs, such as the back, should be favoured, and that care should be taken on implantation to place transponders subcutaneously and not intramuscularly. They conclude that extreme caution should be exercised when using transponders, but that they may affect long-term survival of birds less than do flipper-bands. This single advantage may well outweigh the disadvantages listed above.

Worldwide, we are aware of nine research groups currently investigating the efficacy of transponders for marking penguins in field studies, or comparing this technique with the use of flipper-bands. With the study species' name in parentheses after each locality, these are as follows:

1. Y. Le Maho and colleagues, Crozet Island (King Penguin) (Froget *et al*. 1998);
2. C.O. Olsson and colleagues, South Georgia (King Penguin);
3. K. Kerry and J. Clarke, Mawson, Antarctica (Adélie Penguin);
4. S.G. and W.Z. Trivelpiece, King George Island, Antarctica (Adélie and Gentoo Penguin);
5. Taronga Zoo, Sydney (Little Penguin) (no name given, cited in Fraser & Trivelpiece 1994);
6. Phillip Island, Victoria, Australia (Little Penguin) (Chiaradia & Kerry 1999, Dann *et al*. 2000);
7. R. Wallace, Algarrobo, Chile (Humboldt Penguin *Spheniscus humboldti*);
8. R.J.M. Crawford, Robben Island, South Africa (African Penguin);
9. D.G. Ainley and colleagues, Ross Island, Antarctica (Adélie Penguin) (Ballard *et al*. 2001).

Of these studies, the Phillip Island study suggests that total recoveries of flipper-banded birds over a 6-year period was 81% of the corresponding value for birds carrying only transponders, and that survival is most influenced by flipper-bands in the year immediately after banding (P. Dann, unpublished data; Dann *et al*. 2000).

Conclusion

Subcutaneous transponders do not alter a penguin's hydrodynamic profile, but may result in long-term infection, migrate, be lost or fail, and are less convenient for researchers than are easily visible flipper-bands. However, the majority of studies that we review suggest that flipper-bands carry high long-term costs to their wearers, manifested in the reduced annual survival and breeding success reported for five out of six species studied. This evidence notwithstanding, flipper-bands continue to be used in ecological and, particularly ironically, in conservation-related studies of penguin species upon which their impact has not been assessed. Improvement of band design may reduce the above costs to levels imperceptible to penguins, but we doubt this because even slight increases in drag coefficient probably cause snowball effects that exaggerate reductions in penguin foraging efficiency. The debate about flipper-band design should be replaced by one about the best way to implement alternative marking programmes that do not carry such costs to the birds being studied and to the quality of the data being collected.

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