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When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints

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Abstract Current guidelines for instrumenting birds state that external devices should not exceed 3–5% of the birds' body mass; however, the energetic consequences of carrying any given device mass are likely to vary according to the morphology and ecology of the species concerned. We used a freeware program to estimate the mechanical power requirements of flight at the minimum power speed for 80 species of flying seabird from 8 major groups with payloads of increasing mass. Devices representing 3% of the bird's body mass resulted in an increase in energy expenditure for flight ranging from 4.67 to 5.71% without accounting for the increase in body drag coefficient associated with external devices. This effect differed within and between seabird lineages with members of the Alcidae and Phalacrocoracidae experiencing the highest energetic costs of any increase in device mass. We propose that device effects on seabirds could be further reduced through consideration of species-specific effects of added payload and drag.

Introduction

Animal-attached devices have immensely enhanced our knowledge about free-living animals (e.g. Gillespie 2001; Wikelski et al. 2007; Rutz and Hays 2009) and especially in marine animals, which, though often conspicuous, are difficult to observe continuously (Gauthier-Clerc and Le Maho 2001; Burger and Shaffer 2008). Not only do such devices provide essential information on the biology and ecology of marine species and their role in the oceans (Croxall 1987), but they may also provide quantitative data on a range of physical parameters (Furness and Camphuysen 1997; Fedak 2004; Piatt et al. 2007), leading to a better understanding of what governs animal distribution within marine ecosystems (e.g. Fraser and Trivelpiece 1996; Huettmann and Diamond 2001; Yen et al. 2004). In an age where technological advances are enabling the instrumentation of an increasing number and diversity of animals (e.g. Ropert-Coudert and Wilson 2005), the need to prevent such devices from deleteriously affecting the bearers is particularly pertinent. This is particularly challenging for seabirds that generally move in two different media, air and water, so that devices may compromise both aerodynamic and hydrodynamic performance. In fact, although attempts have been made to quantify some of the deleterious effects of attached tags on animals swimming underwater (e.g. Bannasch et al. 1994; Culik et al. 1994; Watson and Granger 1998; Hazekamp et al. 2010), there is little systematic attempt to quantify how attached devices may affect flying birds (but see Obrecht et al. 1988). Indeed, not having a theoretical basis for understanding the effects of devices has made the question of what exactly constitutes 'deleterious' to remain controversial. For example, whereas an equipped bird experiencing mass loss of 2–3% over 24 h was considered to constitute a serious negative impact on Thick-billed murres (*Uria lomvia*) for Paredes et al. (2005), Benvenuti et al. (1998) considered that a body mass loss of 2–5% over 24–48 h was not drastic. Device impacts can be

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manifested in different ways: behavioural (e.g. Pietz et al. 1993; Paredes et al. 2005; Ropert-Coudert et al. 2007), energetic (e.g. Culik and Wilson 1991; Schmid et al. 1995) and via changes in time constraints (see Culik and Wilson 1992) in addition to physical injuries (e.g. Greenwood and Sargeant 1973; Buehler et al. 1995; Wilson and McMahon 2006). Some behavioural abnormalities can be fairly readily assessed (Wilson and Wilson 1989; Blanc and Brelurut 1997; Bowman and Aborn 2001), as can physical injury (Perry 1981; Tuyttens et al. 2002; Zschille et al. 2008), but determining how attached devices impact the energetics of their carriers is more problematic.

The energetics of birds may be directly affected by externally attached devices in two primary ways. Birds must either expend extra energy countering both the additional mass (e.g. Gessaman and Nagy 1988; Croll et al. 1992) and the increased drag (Culik and Wilson 1991, 1992; Croll et al. 1992; Culik et al. 1994) or decrease some aspects of their performance, such as speed (e.g. Wilson et al. 1986; Ropert-Coudert et al. 2007). Over long deployments such behavioural and energetic changes may affect the individual's fitness, survival and/or reproductive success (e.g. Paquette et al. 1997; Naef-Daenzer et al. 2001; Reynolds et al. 2004; Saraux et al. 2011.

In recognition of the generic disturbance caused by the attachment of external devices, scientists usually comply with two generally accepted recommendation that the weight of the devices should not exceed 3% of a bird's body mass (Kenward 2001) and their cross-sectional area which should be more than 1% of the bird cross-sectional area (Ballard et al. 2001). The "3% rule", which is of particular importance when working with flying birds, is, however, based on scattered observations of various deleterious effects of external devices although consideration of the effect on energetics is conspicuously absent. This stems primarily from the difficulty in measuring the energy expenditure of free-living birds (cf. Butler et al. 2004), particularly as it relates to activity-specific metabolic rate.

In this study, we address the paucity of literature on the effects of attached devices on the energetics of flying birds by using a web-based program (Flight 1.22 software—Pennycuick 2008) on a particular bird group (seabirds) to model the energy expended by birds flying with and without extra payloads. We also aim to highlight one of the main potential weaknesses of the current "3% rule", which is to be solely concerned with device mass, by incorporating the effect of drag resulting from externally mounted devices. Specifically, the software allowed us to differentiate drag caused by an increase in the frontal cross-sectional area from the drag caused by the disruption airflow around a bird's body.

Materials and methods

'Flight' freeware

The Flight program (version 1.22) developed by Colin Pennycuick (Pennycuick 2008) (freeware available online at http://www.bristol.ac.uk/biology/person/index.html?personKey=RIrQ8oVexHK6EF05I9M3ltStjXBnxt) has been used in one form or another by various authors (e.g. Kvist et al. 2001; Norberg and Winter 2006; Tieleman et al. 2008; Xirouchakis and Andreou 2009) and was used to simulate the flight costs of different species of seabirds. This software uses aeronautical theory to estimate the flight parameters of any bird. The user inputs morphological parameters (including body mass, wing span and wing area) and environmental parameters (i.e. air density). Morphometric data are available in the program for a range of species (referred as 'preset birds' on the setup screen), but it is also possible to enter morphometric data for additional species. These data are used to generate a curve of power against speed.

Device mass effect

The aim of this study was to determine the energetic cost of flight in terms of mechanical power by birds carrying different payload masses. This is made possible because the software allows the users to specify a payload mass, separate to the bird body mass. Where the data were available, calculations were performed using the seabird species in 'preset birds'. Morphometric data for additional species were also used, hereafter referred to as 'user birds' in order to enhance the sample size. Note that the term 'bird' refers to a representative individual of a particular bird species and for which the morphometric parameters are mean values calculated from data collected on adults of both sex. A total sample of 80 species, 10 species from each of 8 major lineages of flying seabirds (Alcidae, Diomedeidae, Hydrobatidae, Laridae, Phalacrocoracidae, Procellariidae, Sternidae and Sulidae) were examined (Table 1). For each group of seabirds, we attempted to choose a wide body mass spectrum since body mass affects the energetics of flight substantially (Klaassen 1996; Jenni and Jenni-Eiermann 1998; Hambly et al. 2004b). The morphological parameters of the 'user birds' were taken from Del Hoyo et al. (1992, 1996), Snow et al. (1998), Harrison (1983) and http://www.bto.org/birdfacts/index.htm. All calculations used an air density of 1.22 kg m^{-3}.

Information on wing area or aspect ratio (see Pennycuick 2008 for definitions) is required in order to enter new species into the program. Measurements of wing area and aspect ratio are rare in the literature, whereas measurements of span are more readily available. Therefore, we calculated an index that would allow us to derive the wing area from

Table 1 List of the species of seabirds examined in the study sorted by family and presenting the body mass used for the analysis and the average (X ± SE) ratio between wing span and wing area (units: per metre) used to derive the wing area from the wing span when required

Family	Species name	Body mass (kg)	Mean ratio wing span to wing area
Hydrobatidae	**European Storm-petrel (*Hydrobates pelagicus*)**	0.03	X ± SE = 18.55 ± 1.29 m^{-1}, $N = 5$
	Grey-backed Storm-petrel (*Garrodia nereis*)	0.03	
	Wilson's Storm-petrel (*Oceanites oceanicus*)	0.03	
	Black-bellied Storm-petrel (*Fregatta tropica*)	0.07	
	Least Storm-petrel (*Halocyptena microsoma)*	0.02	
	Leach's Storm-petrel (*Oceanodrona leucorhoa)*	0.04	
	White-faced Storm-petrel (*Pelagodroma marina)*	0.05	
	Fork-tailed Storm-petrel (*Oceanodroma furcata)*	0.06	
	White-bellied Storm-petrel (*Fregatta grallaria)*	0.06	
	Tristram's Storm-petrel (*Oceanodroma tristrami)*	0.08	
Procellariidae	**Antartic prion (*Pachyptila desolata*)**	0.16	X ± SE = 10.98 ± 0.65 m^{-1}, $N = 7$
	Cape petrel (*Daption capensis*)	0.42	
	Northern fulmar (*Fulmaris glacialis*)	0.85	
	White-chinned petrel (*Procellaria aequinioctialis*)	1.23	
	Northern giant petrel (*Macronectes halli*)	3.80	
	Grey petrel (*Procellaria cinerea*)	1.00	
	Antarctic petrel (*Thalassoica antarctica*)	0.68	
	Soft-plumaged petrel (*Pterodroma mollis*)	0.31	
	Flesh-footed shearwater (*Puffinus carneipes*)	0.57	
	Southern giant petrel (*Macronectes giganteus*)	4.50	
Sternidae	**Brown noddy (*Anous stolidus*)**	0.17	X ± SE = 11.37 ± 0.62 m^{-1}, $N = 3$
	Sooty tern (*Sterna fuscata*)	0.20	
	Little tern (*Sterna albifrons*)	0.06	
	Royal tern (*Thalasseus maximus*)	0.45	
	Artic tern (*Sterna paridisea*)	0.10	
	Caspian tern (*Sterna caspia*)	0.65	
	White-winged black tern (*Childonias leucopterus*)	0.06	
	Black tern (*Childonias niger*)	0.07	
	Forster's tern (*Sterna forsteri*)	0.16	
	Bridled tern (*Sterna anaethetus*)	0.14	
Alcidae	**Razorbill (*Alca torda*)**	0.66	X ± SE = 14.52 ± 0.50 m^{-1}, $N = 4$
	Common guillemot (*Uria aalge*)	0.86	
	Atlantic puffin (*Fratercula artica*)	0.40	
	Black guillemot (*Cephus grylle*)	0.45	
	Little auk (*Alle alle*)	0.15	
	Pigeon guillemot (*Cepphus columba*)	0.51	
	Tufted puffin (*Fratercula cirrhata*)	0.78	
	Thick-billed murre (*Uria lomvia*)	1.12	
	Horned puffin (*Fratercula corniculata*)	0.61	
	Least auklet (*Aethia pusilla*)	0.09	
Phalacrocoracidae	**Great cormorant (*Phalacrocorax carbo*)**	2.53	X ± SE = 6.29 ± 0.12 m^{-1}, $N = 4$
	Common shag (*Phalacrocorax aristotelis*)	1.75	
	Double-crested cormorant (*Phalacrocorax auritus*)	1.51	
	Imperial shag (*Phalacrocorax atricep*)	2.23	
	Bank cormorant (*Phalacrocrax neglectus*)	1.80	
	Long-tailed cormorant (*Phalacrocrax africanus*)	0.68	
	Spotted shag (*Phalacrocorax punctatus*)	0.96	

Table 1 continued

Family	Species name	Body mass (kg)	Mean ratio wing span to wing area
	Japanese cormorant (*Phalacrocorax capillatus*)	2.80	
	Red-faced cormorant (*Phalacrocorax urile*)	2.10	
	Little black cormorant (*Phalacrocorax sulcirostris*)	0.87	
Sulidae	**Red-footed booby (*Sula sula*)**	1.05	$X \pm SE = 7.46 \pm 0.23\ m^{-1}$, $N = 3$
	Brown booby (*Sula leucogaster*)	1.15	
	Northern gannet (*Morus bassana*)	2.11	
	Cape gannet (*Morus capensis*)	2.60	
	Blue-footed booby (*Sula nebouxii*)	1.55	
	Australasian Gannet (*Morus serrator*)	2.00	
	Masked booby (*Sula dactylatra*)	1.79	
	Nazca booby (*Sula granti*)	1.30	
	Abbott’s booby (*Sula abbotti*)	1.46	
	Peruvian booby (*Sula variegata*)	1.41	
Laridae	**Black-legged kittiwake (*Rissa tridactyla*)**	0.39	$X \pm SE = 7.65 \pm 0.59\ m^{-1}$, $N = 7$
	Black-headed gull (*Larus ridibundus*)	0.29	
	Lesser black-backed gull (*Larus fuscus*)	0.80	
	Herring gull (*Larus argentatus*)	0.86	
	Great blac-backed gull (*Larus marinus*)	1.52	
	Kelp gull (*Larus dominicanus*)	1.11	
	Black-billed gull (*Larus bulleri*)	0.23	
	Heermann’s gull (*Larus heermannii*)	0.51	
	Ivory gull (*Pagophila eburnea*)	0.61	
	Common gull (*Larus canus*)	0.43	
Diomedeidae	**Black-browed albatross (*Diomedea melanophris*)**	3.15	$X \pm SE = 5.79 \pm 0.41\ m^{-1}$, $N = 3$
	Grey-headed albatross (*Diomedea chrysostoma*)	3.60	
	Sooty Albatross (*Phoebetria fusca*)	2.50	
	Light-mantled albatross (*Phoebetria palbebrata*)	3.00	
	Black-footed albatross (*Phoebastria nigripes*)	3.10	
	Laysan albatross (*Phoebastria immutabilis*)	2.85	
	Shy albatross (*Thalassarche cauda*)	3.90	
	Atlantic yellow-nosed albatross (*Thalassarche chlororhynchus*)	2.20	
	Waved albatross (*Phoebastria irrorata*)	3.40	
	Salvin’s albatross (*Thalassarche salvini*)	3.59	

Shown in bold are the names of the ‘preset birds’ and in normal, the names of the ‘own birds’

the wing span systematically for morphologically similar species. This index was the wing span divided by the wing area (units: per metre) which is the reciprocal of the mean chord. We used the ‘preset bird’ data from the Flight program to calculate this index of wing area to wing span for birds within any one family. This index was taken from a mean calculated for a minimum of 3 ‘preset bird’ for each of the major groups of seabird examined (Table 1). Of the total of 80 birds examined, 29 were ‘preset birds’ and 51 were ‘own birds’.

In this study, we examined the mechanical power required for birds to fly at their calculated minimum power speed (V_{mp}) which is the air speed at which the least power is required from the flight muscles (Pennycuick 2008). This variable was selected as it was considered to be one of the variables most broadly applicable to the range of seabird species examined. All further references to power are to estimates of the mechanical rather than chemical power. The flight mechanical power was calculated for a given flight speed which corresponds to the speed of the bird relative to the air (which may or may not be moving relative to geographic coordinates, as in wind, for example) and therefore does not correspond to groundspeed (except where wind speed = 0). In addition, the mechanical power appeared not to be affected by the flight style of the birds since by definition, for the calculation of flight power, the program only considers continuous flapping flight (rather than bounding flight for example). The power at V_{mp} was computed for 6 different scenarios of payload mass: (1) birds with no payload, (2) birds with a payload that represented 1%, (3) 2%, (4) 3%, (5) 4%, or (6) 5% of the bird's body mass.

The increase in power at V_{mp} was also calculated per kilo of body mass in order to enable comparisons of payload effect across species of variable body mass. The mean of the mass-specific power at V_{mp} was determined for each seabird family, and its variation was assessed with respect to the load added to the birds. We calculated the gradients and the intercepts from regressions of the mass-specific power at V_{mp} and the size of the load, and these were examined as a function of the body mass using Spearman's correlation (r_s). We considered this at the family level (using the 10 species per family) as well as over the whole data set or over the following different groups of families: the group including Hydrobatidae, Procellariidae, Sternidae, Sulidae, Laridae and Diomedeidae and the group formed by Alcidae and Phalacrocoracidae.

Device drag effect

All calculations were initially made considering that the birds were equipped with a perfectly streamlined device, with the extra drag resulting only from an increase in the frontal cross-sectional area of the bird. This was obtained by using the default value of 1 set by the program for the payload drag factor which means that the bird's body drag coefficient remained unchanged. To get a more realistic view, however, we also calculated for one species of each family (i.e. 8 species in total) the mechanical power to fly at V_{mp} for a non-streamlined device which would increase the bird body drag coefficient by a factor of 1.5 (the factor is derived from unpublished data of drag measurements we collected in a wind tunnel on a bird model wearing different-sized squares). The calculations were performed for a non-streamlined payload weighing 3% of the bird's body mass. The percentage of increase in the flight cost between the non-streamlined scenario and the unequipped scenario was determined and compared with the percentage increase in flight cost observed between a streamlined scenario (for a payload weighing 3% of the bird's body mass) and the unequipped scenario.

All the tests were performed using Minitab (MINITAB® Release 14.1 version 2003) and had a significance threshold of $P < 0.05$.

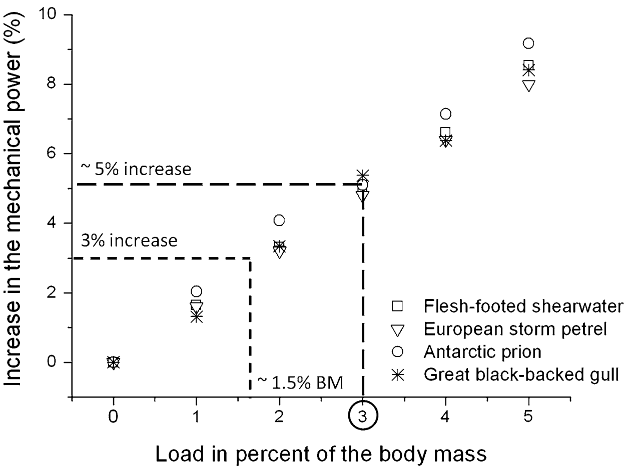

Fig. 1 Examples of the mechanical power at V_{mp} used by different seabird species during flight (expressed as a percentage of the power required for unequipped flight at V_{mp}) as a function of the extra mass carried. The *dashed lines* show how loads amounting to ca. 1.5 and 3% of bird body mass equate to ca. 3 and 5% increases in mechanical power, respectively

Results

The calculated power for flying at V_{mp} in unequipped birds varied between 0.12 W (for the least storm-petrel *Halocyptena microsoma* smallest) and 49.8 W (for the grey-headed albatross *Diomedea chrysostoma*). Addition of payloads increased the level of power required to fly as a function of payload mass. Specifically, the additional mechanical power expended by a bird carrying a device (expressed as a percentage of the unequipped mechanical power at V_{mp}) increased linearly with device mass (also expressed as a percentage of body mass), with values for devices weighing 1% of bird body mass inducing increases between 1.3% (great black-backed gull *Larus marinus*) and 2.0% (antartic prion *Pachyptila desolata*), and devices weighing 5% of body mass inducing increases between 8% (European storm-petrel *Hydrobates pelagicus*) and 9.2% (antarctic prion *Pachyptila desolata*) (cf. Fig. 1). With respect to devices weighing 3% of bird body mass, an increase in flight cost ranging from 4.67% for the light-mantled albatross (*Phoebetria palbebrata*) and 5.71% for the blue-footed booby (*Sula nebouxii*) was observed.

Combination of mass-specific power at V_{mp} from all species into mean mass-specific values for families showed that mass-specific power at V_{mp} increased with payload mass at the family level but that slopes and intercepts varied between families (Fig. 2; Table 2). Auks and cormorants had the highest mass-specific power at V_{mp} of the families considered and also the steepest gradients in

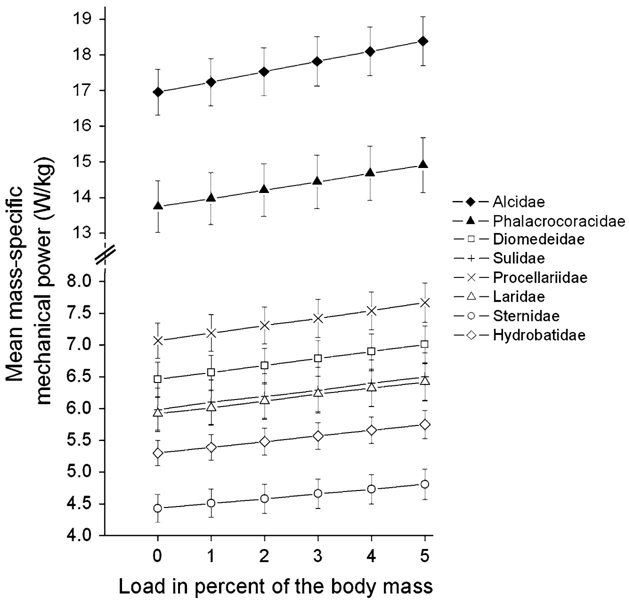

Fig. 2 The mean mass-specific mechanical power at V_{mp} calculated for 10 species from eight major groups of seabird as a function of the payload mass (expressed as a percentage of the body mass). *Bars* show standard error. Gradients and intercepts of the regression are shown in Table 2

response to payload. Terns had the lowest values in mass-specific power at V_{mp} and the shallowest gradients. Body mass appeared to affect both gradient and intercept in some instances (Fig. 3) with a significant relationship found between intercept and body mass for the Procellariidae and the Laridae (Spearman's rank correlation, $r_s = 0.72$, $N = 10$, $P = 0.02$ and $r_s = 0.70$, $N = 10$, $P = 0.03$, respectively; Fig. 3b plain lines). In the analysis involving all birds from eight families (i.e. 80 species as one group), there was a significant positive correlation between both gradient and intercept and body mass (Spearman's rank correlation, $r_s = 0.41$, $N = 80$, $P < 0.001$; $r_s = 0.42$, $N = 80$, $P < 0.001$ for the gradient and intercept, respectively). Consideration of just auks and cormorants together yielded no correlation in either gradient or intercept (Spearman's rank correlation, $r_s = -0.43$, $N = 20$, $P = 0.06$; $r_s = -0.44$, $N = 20$, $P = 0.05$ for the gradient and intercept, respectively) although both were significant when all six other families were grouped (Spearman's rank correlation, $r_s = 0.58$, $N = 60$, $P < 0.001$; $r_s = 0.59$, $N = 60$, $P < 0.001$ for the gradient and intercept, respectively, Fig. 3a, b dashed lines).

The mean difference in flight mechanical power at V_{mp} found between the streamlined and the non-streamlined scenarios was X ± SE = 11.5 ± 0.6%, $N = 8$ and ranged from X ± SE = 10.4 ± 0.2%, $N = 10$ for the black-browed albatross (*Diomedea melanophris*) to X ± SE = 16.9 ± 3.2%, $N = 10$ for the common guillemot (*Uria aalge*) (Table 3).

Discussion

Over the past 20 years, devices have been deployed on an increasing number and diversity of free-living animals (Ropert Coudert et al. 2009; Barron et al. 2010), necessitating a broader understanding of the deleterious effects of such devices, and how they may be minimised (Murray and Fuller 2000; Godfrey and Bryant 2003; Barron et al. 2010). Among the different features of external devices that can affect birds are the mass (cf. Phillips et al. 2003), the shape (cf. Culik et al. 1994), the position (cf. Chiaradia et al. 2005) and even the colour of the equipment (Wilson et al. 1990). This study concentrates on the effects of mass of an added payload, although devices are also likely to result in an increase in the body drag coefficient of the bird (cf. Obrecht et al. 1988; Bannasch et al. 1994) caused by the disruption of the airflow around the body (Pennycuick 2008). Even when the payload is assumed to be well-streamlined, the software does incorporate the increase in cross-sectional area of the subject animal due to the device.

Mass is critical for flying birds because it changes bird energetics (e.g. Cairns et al. 1987; Gessaman and Nagy

Table 2 Mean gradient and intercept obtained from the regressions between the mass-specific mechanical flight power at V_{mp} and the payload mass calculated for each of the eight groups of seabird included in this study (see Fig. 2)

Family	Gradient	Intercept
Sternidae	X ± SE = 0.07 ± 0.01, $N = 10$	X ± SE = 4.43 ± 0.69, $N = 10$
Hydrobatidae	X ± SE = 0.09 ± 0.01, $N = 10$	X ± SE = 5.30 ± 0.63, $N = 10$
Laridae	X ± SE = 0.10 ± 0.02, $N = 10$	X ± SE = 5.92 ± 0.83, $N = 10$
Sulidae	X ± SE = 0.10 ± 0.02, $N = 10$	X ± SE = 5.99 ± 0.99, $N = 10$
Diomedeidae	X ± SE = 0.11 ± 0.01, $N = 10$	X ± SE = 0.50 ± 0.83, $N = 10$
Procellariidae	X ± SE = 0.12 ± 0.01, $N = 10$	X ± SE = 6.99 ± 0.91, $N = 10$
Phalacrocoracidae	X ± SE = 0.23 ± 0.04, $N = 10$	X ± SE = 13.74 ± 2.26, $N = 10$
Alcidae	X ± SE = 0.29 ± 0.03, $N = 10$	X ± SE = 16.95 ± 2.05, N = 10

The species are sorted in ascending order in terms of energetic impact of the payload. This table provides an easy way for researchers to estimate the mass-specific power at V_{mp} for any seabird species belonging to one of the illustrated families during flight when equipped with a given payload

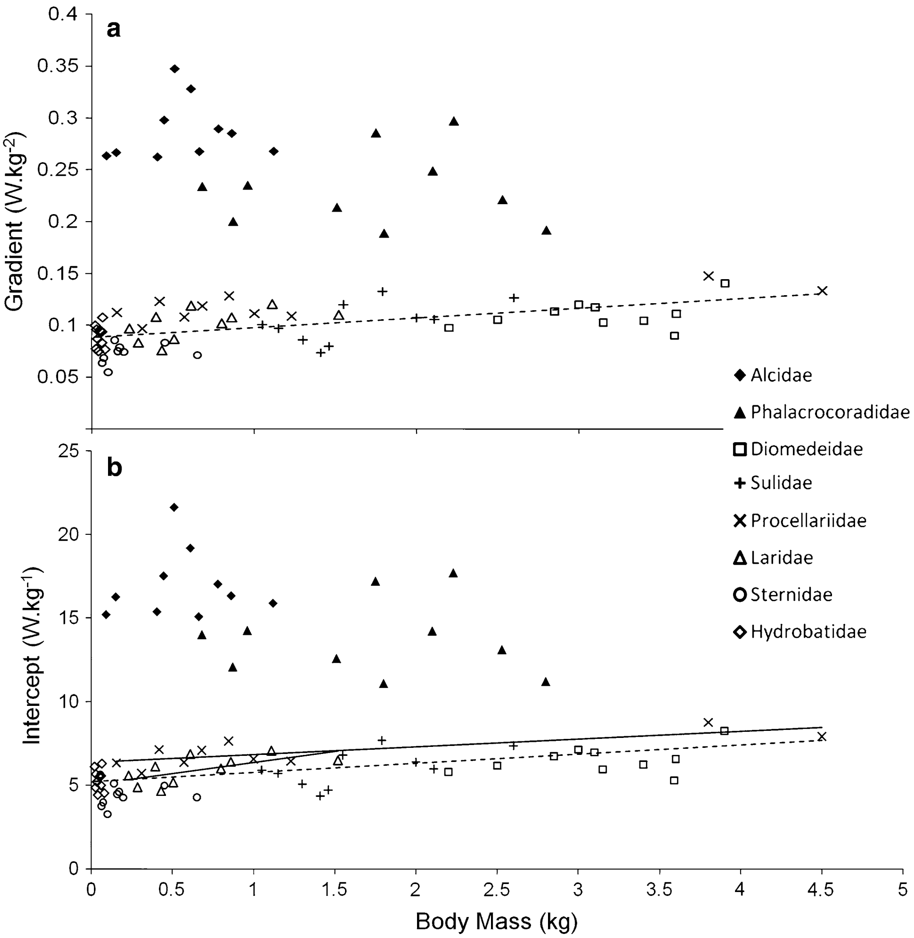

Fig. 3 The gradient (**a**) and the intercept (**b**) obtained from the regression between the mass-specific mechanical power for flight at V_{mp} and the extra mass added to a bird (see Fig. 2; Table 2) for each of the 10 species from the 8 major groups of seabirds considered in this study as a function of body mass. *Each point* represents a species from a particular seabird family denoted by the symbol. Only the significant Spearman's rank correlations between the body mass (*X*-axis) and either the slope (*Y*-axis in Fig. 3a) or the intercept (*Y*-axis in Fig. 3b) are shown. The linear regression equations are $y = 0.0046x + 0.1341$ (group including Hydrobatidae, Procellariidae, Sternidae, Sulidae, Laridae and Diomedeidae; dashed line Fig. 3a), $y = 1.3301x + 5.0207$ (Laridae; *short plain line* Fig. 3b), $y = 0.4589x + 6.3727$ (Procellariidae; *long plain line* Fig. 3b), $y = 0.2646x + 7.9208$ (group including Hydrobatidae, Procellariidae, Sternidae, Sulidae, Laridae and Diomedeidae; *dashed line* Fig. 3b)

1988; Massey et al. 1988; Hooge 1991; Passos et al. 2010). This is highlighted in migratory birds which limit the amount of fuel they store because increases in body mass lead to a concomitant increase in the cost of transport (Pennycuick 1989). Although scientists may attempt to minimize device mass problems, and particularly behavioural aberrations, by complying with the recommended limit of 3% of the bird's body mass as suggested by Kenward in (2001), there is little information on how device mass affects bird energetics. Cairns et al. (1987) report an increase of 6.1% in the flight costs of common guillemots fitted with units representing about 2.5% of the bird's body mass, and this is similar to estimates from our study where, for the 80 species examined, a payload of 3% of the bird's body mass increased energetic cost of flight by approximately 5%. In fact, a 3% in increase in payload does not translate into a simple 3% increase in energetic flight costs. Conversely, no energetic effect of payload was found by Nudds and Bryant (2002) working on zebra finches (*Taeniopygia guttata*) carrying an extraordinary 27% additional mass. Errors in the doubly labelled water methodology (for review see Nagy 1980; Butler et al. 2004) used in this study, which can lead to high variance in estimates (e.g. Schultner et al. 2010; Shaffer 2010), may be responsible for this. The zebra finch study also only incorporated routine short flights performed between two perches in an aviary and much of the variance presumably stemmed from the way birds partitioned other activities.

Based on Flight's model calculations (Pennycuick 2008), we also assessed the potential effect of extra mass on the energetic expenditure of flying birds by looking at the gradient of the regression between amount of load and

Table 3 Mechanical power to fly at V_{mp} for unequipped birds, birds equipped with a streamlined payload (i.e. the bird drag coefficient remains unchanged) and birds with a non-streamlined payload (i.e. the bird drag coefficient is increased by a factor of 1.5—see text)

Species	Scenario	Mass-specific flight mechanical power cost (W/kg)	Increase in flight mechanical power cost compared to unequipped scenario (%)
Black-browed albatross (*Diomedea melanophris*)	Unequipped bird	5.94	–
	Streamlined device	6.03	5.35
	Non-streamlined device	6.16	16.04
Sooty tern (*Sterna fuscata*)	Unequipped bird	4.27	–
	Streamlined device	4.34	5.02
	Non-streamlined device	4.41	16.15
Black-legged kittiwake (*Rissa tridactyla*)	Unequipped bird	6.12	–
	Streamlined device	6.22	5.39
	Non-streamlined device	6.32	16.60
Wilson's storm petrel (*Oceanites oceanicus*)	Unequipped bird	5.19	–
	Streamlined device	5.28	5.03
	Non-streamlined device	5.36	16.20
Northern fulmar (*Fulmarus glacialis*)	Unequipped bird	7.65	–
	Streamlined device	7.77	4.95
	Non-streamlined device	7.90	16.23
Brown booby (*Sula leucogaster*)	Unequipped bird	5.70	–
	Streamlined device	5.79	5.04
	Non-streamlined device	5.89	16.34
Great cormorant (*Phalacrocorax carbo*)	Unequipped bird	13.12	–
	Streamlined device	13.32	4.82
	Non-streamlined device	13.56	16.27
Common guillemot (*Uria aalge*)	Unequipped bird	7.22	–
	Streamlined device	7.33	4.98
	Non-streamlined device	7.46	22.83

For the device scenarios, the flight mechanical power costs were calculated for payloads weighing 3% of the bird's body mass. The results are given for just one species from each of the eight seabird families examined in this study

energy expenditure. Highest gradients correspond to the greatest effect of extra payload mass. This is in addition to the difference in the amount of power required to fly unencumbered between species, as shown by the variation in intercept (corresponding to no payload) (Fig. 2 and Table 2) and which presumably results from morphological differences as well as from variation in wing kinematics and flight styles (e.g. Dial et al. 1997; Rayner 1999; Tobalske et al. 2003). Here, our analysis indicates that bird energetic response to payload during flight seems to depend critically on species and group (Figs. 2, 3), probably due to differences in morphology, behaviour and ecology (cf. Pennycuick 1987). Flapping flight is one of the most energetically expensive modes of locomotion for vertebrates (Norberg 1990; Hedenström 1993; Rayner 1993), which explains why continuously flapping birds generally have higher energy expenditure than gliding or partially gliding (glide-flappers or flap-gliders) birds (e.g. Birt-Friesen et al. 1989; Klaassen 1996). Our results are consistent with this since auks and cormorants, which are continuous flappers (Pennycuick 1987; Spear and Ainley 1997), appeared to have the most energetically expensive flight at V_{mp} (cf. differences in the intercept; Table 2). These two sets of species also appeared to be the most impacted by the payload mass (cf. differences in the gradient; Table 2). However, we noticed that other flapping species such as gulls and terns showed an energetic flight cost at V_{mp} similar to the species using partial gliding such as storm-petrels, procellarids and gannets/boobies (Pennycuick 1987; Spear and Ainley 1997). Thus, flight mode is unlikely to be the only parameter to affect payload-based flight energetics.

Various foraging strategies have been documented for different seabird species, ranging from surface feeders to pursuit divers (Cramp and Simmons 1983; Harper et al. 1985). Efficient diving is at odds with efficient flight (Wilson et al. 1992). Morphological adaptations for diving

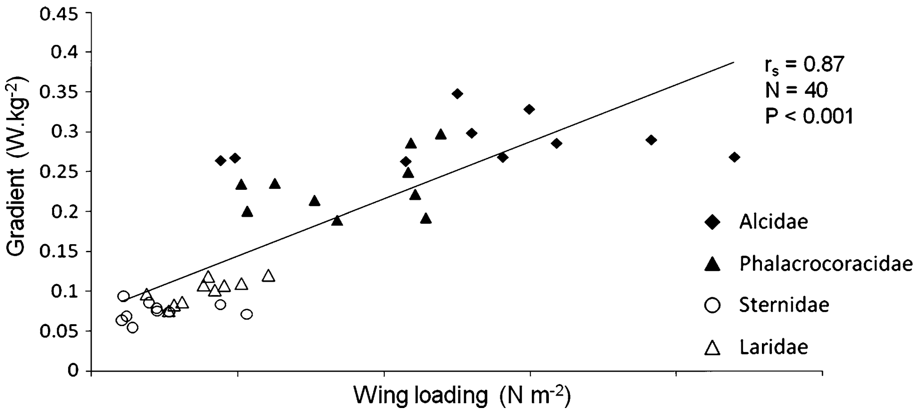

Fig. 4 The gradient obtained from the regression between the mass-specific flight mechanical power at V_{mp} and the extra mass added to a bird (see Fig. 2; Table 2) for each of the 4 families of flappers considered in this study as a function of their wing loading. Each point represents a species from a particular seabird family denoted by the symbol. The line indicates a significant correlation between wing loading and gradient

such as an increase in muscle mass and blood volume (Lovvorn and Jones 1994) and wettable plumage (Mahoney 1984; Ribak et al. 2005; Ortega-Jiménez et al. 2010) generally result in higher body masses which, associated with the reduced size of the wings (Storer 1960; Rayner 1988; Lovvorn and Jones 1994) lead to an increase in wing loading and therefore higher flight energy expenditure (Pennycuick 1987, 1989; Norberg 1990). The substantial adaptations to diving displayed by auks and cormorants (Pennycuick 1987; Hodum et al. 1998; Watanabe et al. 2011) in part explain their high power costs for flight as well as their apparent sensitivity to payloads. In fact, there is a significant positive correlation between wing loading and the gradient of the mass-specific mechanical power for flight *versus* payload mass for the four families of flapping species examined in this study (Fig. 4, Spearman's rank correlation, $r_s = 0.87$, $N = 40$, $P < 0.001$). More precisely, auks and cormorants, which had the highest wing loadings (mean wing loadings of $X \pm SE = 131.6 \pm 0.3$ N m^{-2}, $N = 10$ and $X \pm SE = 89.0 \pm 0.2$ N m^{-2}, $N = 10$, respectively), also had steeper gradients than gulls or terns (mean wing loadings of $X \pm SE = 38.2 \pm 0.1$ N m^{-2}, $N = 10$ and $X \pm SE = 23.5 \pm 0.07$ N m^{-2}, $N = 10$), strongly suggesting that wing morphology and body mass are key factors in modulating the impact of payloads on the flight energetic of seabirds.

The issue of how bird mass affects the energetics of flight in device-equipped birds in general has been previously discussed by Tucker (1977) and Caccamise and Hedin (1985), who noted that device mass impacts larger birds more because heavier birds have less 'power surplus'. In a similar manner, large migratory birds using flapping flight face greater energetic costs than small birds (Pennycuick 1972; Klaassen 1996). Our work on flap-gliders also points to larger birds being absolutely more affected by devices, although significant intra-family differences were only apparent in gulls and procellarids, perhaps because individuals from these groups had the broadest range of body mass (from 0.16 to 4.50 kg and from 0.23 to 3.15 kg, respectively) but also because it is likely to be a multifactorial problem. Similarly, Birt-Friesen et al. (1989) noted significant differences in intercepts of regressions of metabolism and body mass in various bird groups, including albatrosses, alcids, diving petrels, gannets, gulls, penguins, procellarids and storm-petrels.

Beyond mass, although the drag associated with tags has been relatively well studied on swimming birds (e.g. Wilson et al. 2004; Ropert-Coudert et al. 2007; Saraux et al. 2011), little is known about the negative impacts of tracking devices attached to flying birds. Despite the lower density of air compared with water, our results indicate that flying birds equipped with non-streamlined devices may have power costs some 17.1 ± 2.3% (mean calculated for the 8 species presented in Table 3) higher than unequipped birds. This is about 3 times higher than the 5.1 ± 0.2% average increase observed between birds equipped with streamlined devices and unequipped birds (mean calculated for the 8 species presented in Table 3). Clearly, consideration of both mass and drag are important in proper formulation of a "3% rule," especially since the devices currently used on birds are unlikely to be perfectly streamlined.

Limitations of the study

Calculations of energy expenditure based on aerodynamic models usually overestimate the measured energetic cost of flight of birds carrying extra load (Kvist et al. 2001; Hambly et al. 2004a; Schmidt-Wellenburg et al. 2007, 2008). One explanation for this is that birds may adjust their behaviour and/or body condition or physiology, so that energy expenditure can remain approximately at the same level in equipped and unequipped birds. This occurs at the expense of other flight parameters, however. Among the main behavioural responses recorded are a decrease in flight speed (e.g. Videler et al. 1988; Hambly et al. 2004a), a decrease in take-off velocity (e.g. Nudds and Bryant 2002) and/or a change in the time spent flying (e.g. Gessaman et al. 1991; Hooge 1991). Although such

Table 4 Examples of flight characteristics other than the flight mechanical power at V_{mp}, computed using the Flight program for a Great cormorant (*Phalacrocorax carbo*), which are predicted to be modified as a consequence of extra mass

	Unequipped bird	Bird with a payload of 5% its body mass	Difference in percentage
Minimum power speed V_{mp} (m s^{-1})	16.5	16.8	1.8↓
Maximum range speed V_{mr} (m s^{-1})	26.4	26.8	1.5↑
Maximum rate of climb (m s^{-1})	0.432	0.411	4.7↑
Maximum effective L/D	13.8	13.7	0.7↓
Wingbeat frequency (Hz)	5.09	5.18	1.7↑

Minimum power speed V_{mp} is the speed for minimum mechanical power in level flight; maximum range speed V_{mr} is the speed at which the effective lift/drag radio is at a maximum; maximum rate of climb is the rate of climb when flying at V_{mp} and exerting maximum power; maximum effective L/D is the value of the effective lift/drag ratio when flying level at the maximum range speed V_{mr}; wingbeat frequency is the wingbeat frequency expected in level flight at V_{mp}

responses ostensibly reduce the energetic cost of flight, they have associated costs, such as reduced foraging efficiency (Gales et al. 1990; Weimerskirch et al. 2000; Navarro et al. 2008) or a decrease their capacity to escape predators (Burns and Ydenberg 2002). Importantly, device effects may vary in relation to deployment duration and the environmental conditions (Wilson and McMahon 2006; Saraux et al. 2011).

Our study examines one flight metric (power), whereas many, if not all, of the flight characteristics of a bird carrying extra mass can be affected, some that are also detailed by the Flight program. For example, a great Cormorant (*Phalacrocorax carbo*) carrying a payload of 5% of its body mass would have its maximum rate of climb reduced from 0.43 to 0.41 m s^{-1} (a drop of 4.7%) show an increase in its minimum power speed from 16.5 to 16.8 m s^{-1} (an increase of 1.8%), incur an increase in the speed at which it has the maximum effective lift-to-drag ratio from 26.4 to 26.8 m s^{-1} (an increase of 1.5%) while the lift-to-drag ratio at V_{mp} would decrease from 13.8 to 13.7 (0.7%) and the wing-beat frequency at V_{mp} would increase from 5.09 to 5.18 Hz (1.7%) (Table 4). The ecological significance of these changes presumably varies according to the species concerned so a case-by-case analysis would seem appropriate.

Our method also assumes that all birds examined can be effectively modelled by the Flight program (Flight 1.22) without taking into account the differences inherent in the way species live. For example, albatrosses and petrels rely heavily on dynamic soaring for efficient flight (Pennycuick 2002) and have energy expenditures for flight that are correlated with wind speed (Calvo and Furness 1992; Furness and Bryant 1996; Bowlin and Wikelski 2008), so the impact of attached devices will presumably vary according to meteorological conditions. Similarly, many gulls use thermal soaring to move (Brown 1963; Croxall 1987), and some seabirds such as shearwaters (Rosén and Hedenström 2001) and cormorants (De la Cueva and Blake 1993) may even use the ground effect. All these behaviours may cause estimated energetic flight costs to vary from those calculated and may even help mitigate the effects of device mass.

Free-living birds routinely have to carry payloads when flying with food in their digestive system or in their beaks or gular pouches (cf. Vermeer 1981; Mehlum and Gabrielsen 1993; Sydeman et al. 1997), either for provisioning their chicks or for self-provisioning. In this respect, our calculations are conservative since we have assumed all birds to be flying empty. The amount of weight carried as food by seabirds generally varies between about approximately 2% for sooty terns (*Sterna fuscata*, Ricklefs and White 1981) to about 15–20% (ignoring non-volant species) for albatrosses although they have been recorded flying with payloads of about 30% of their body mass (Weimerskirch et al. 1997, 2000). We note that incorporation of device mass on top of mass carried as food could prove pivotal for power requirements during flight. For instance, a great cormorant transporting an average food load mass of 330 g (Grémillet et al. 1996) would have to provide 18% more power to fly at V_{mp} than an empty conspecific, and if additionally equipped with a 3% payload, this figure would increase to 22%. Likewise, the amount of time spent in flight per day can vary considerably inter-specifically (e.g. Pelletier et al. 2008; Ryan et al. 2010; Thaxter et al. 2010), so birds that spend little time flying, such as thick-billed murres, which spend on average 7.1% of their time flying (1.7 h per day, Falk et al. 2000), will presumably use relatively less energy per day compensating for device mass than, for example, an albatross such as the grey-headed albatross, which spends up to 74% (up to 13–20 h per day) of its time aloft (Prince and Francis 1984; Afanasyev and Prince 1993). Intraspecific variation in flight duration (e.g. Hull et al. 2001; Ryan et al. 2010) will be affected similarly.

Overall, although the Flight program clearly has its limitations, it does at least give a first assessment of the expected costs of flight for seabirds carrying payloads, which we would argue is markedly more informative than simple adherence to the 3% rule (Kenward 2001). As early as 1985, Caccamise and Hedin (1985) argued that, given the range of variation in load weight based on a fixed percentage of body mass between large birds and small birds, it is inappropriate to apply the same tagging method to all birds. In addition, variation in the amount of time that particular species spend flying, coupled with putative payloads due to food could, and should, be built into assessments of the effect of devices on birds by researchers who can access the Flight program as freeware. Such an approach would allow workers to determine whether their proposed research is likely to compromise the study animal's welfare unacceptably or, at the very least, allow them to consider how, and to what extent, bird ecology, behaviour and welfare might be impacted.

It is unlikely that we will ever be able to put an external device on a free-flying bird without impeding it somewhat (cf. Calvo and Furness 1992), despite the huge advances that are being made in the miniaturization of electronics (Ropert-Coudert and Wilson 2005), but careful consideration of how birds are likely to react to devices can be theoretically accessed via models such as that used in the Flight program. We note that a quantitative treatment of the relationship between device shape, size, placement on the body and the consequences of this for an animal's energy expenditure may require more detailed consideration. Nonetheless, the type of approach taken in this study should bolster visual observations (e.g. Fraser et al. 2002; Garthe et al. 2007; Watanuki et al. 2008) and other quantitative examinations of behaviour (Wilson et al. 1986; Ropert-Coudert et al. 2007), to inform us of the strengths and weaknesses of device systems that we may aspire to use and ultimately give us clues as to their biological utility.

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