PRE-DIVE LEAPS IN DIVING BIRDS; WHY DO KICKERS SOMETIMES JUMP?

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SUMMARY

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The incidence of pre-dive leaps was examined in foraging Cape *Phalacrocorax capensis*, Crowned *P. coronatus* and Whitebreasted *P. carbo* Cormorants and European Coots *Fulica atra*. Cape Cormorants and European Coots showed a positive relationship between the height of the leap and derived water depth. Observations on 37 species of diving birds indicated that wing-propelled species never engage in pre-dive leaps whereas at least 11 of the 14 foot-propelled species examined do. For birds diving to the seabed, vertical, rather than oblique, descents are most efficient because no time or energy is wasted in horizontal movement. Because all seabirds are buoyant, birds up-ending prior to a dive have the wings underwater but not the feet. Wing-propelled species can thus apply thrust to descend vertically without a pre-dive leap. Foot-propelled species use pre-dive leaps to immerse their feet underwater so as to effect an efficient vertical descent. However, the subsequent high descent speed makes this strategy inappropriate when the water is shallow.

INTRODUCTION

Many diving birds leap from the surface of the water to initiate submergence (e.g. Lawrence 1950, Bell 1984). Interspecific variability in the frequency of this behaviour and height of the leap has led some authors to suggest that it might be a useful species diagnostic (Nuechterlein 1981, Casselton 1986). Subsequently, it has been shown that there is great intraspecific variability in pre-dive leaping behaviour and that high leaps are more likely to occur when wave action is higher (Forbes & Sealy 1988) and when water is deeper (Forbes & Sealy 1988, Nuechterlein & Buitron 1989). Neuchterlein & Buitron (1989) conclude that birds engaging in pre-dive leaps are able to use the momentum of their body mass in air to provide a greater initial downward thrust to the dive. This is not entirely consistent because the thrust that a leaping bird has to apply to the water in order to become airborne is the same as the thrust applied to the surface of the water at the moment of re-entry. Why then, do birds leap?

We examined the occurrence of leaping in a number of bird species, diving at sea, according to parameters that we felt might be relevant. In this paper we present the results of this study and consider when it is advantageous for diving birds to perform pre-dive leaps.

MATERIALS AND METHODS

Most field work was conducted between 11 and 19 August 1989 on Cape *Phalacrocorax capensis*, Crowned P. *coronatus* and Whitebreasted P. *carbo*

Cormorants at Saldanha Bay (33 03S, 17 58E), South Africa and between 15 January and 15 March 1991 on European Coots *Fulica atra* in the Kiel Fiord (54 20N, 10 10E), Baltic Sea, Germany. The water in which the coots were diving was ranked 'shallow', 'deep' or 'intermediate' and delineated by buoys used by boaters. We could not, however, ascertain the specific depth of the various depth categories since we had no boat available.

Solitary diving birds were observed through 8x40 binoculars until they submerged. The manner in which the birds submerged was then classified into one of three catagories similar to those used by Nuechterlein & Buitron (1989):

(1) Flat surface dive: no upward motion was detected so that at no point during submergence was any greater proportion of the body above the surface than when the bird was resting.

(2) Quasi-leap: a clear upward movement was detected before the bird submerged so that momentarily a higher proportion of the body was above the surface than when the bird was resting. However, at no point was the bird completely clear of the water (cf. Hui 1989).

(3) Full leap: the bird leapt completely clear of the water before submerging.

The duration of the ensuing dive was then timed with a stopwatch and recorded to the nearest second. Only one record was obtained for each individual.

Between 1985 and 1991 observations were made on foraging seabirds in and around Antarctica, Australia, Canada, Chile, New Zealand, Norway, South Africa, Sweden and the United Kingdom. We noted whether particular species (Table 1) ever engaged in leaps to effect submergence. No attempt was made to differentiate between quasi-leaps and full leaps. A leap was scored if a clear upward motion was detected before the bird submerged. During these observations dive durations were not systematically noted.

RESULTS

European Coots diving in the Baltic Sea stayed underwater longer with increasing water depth. Mean dive duration for shallow, intermediate and deep water was 2.4 s (SD 2.2, n = 13), 9.2 s (SD 1.5, n = 12) and 15.2 s (SD 3.1, n = 13), respectively. Both Cape Cormorants and European Coots showed a very clear relationship between the tendency to engage in pre-dive leaps and dive duration (Spearman Ranks; $R_s = 0.81$, $P < 0.001$ and $R_s = 0.61$, $P < 0.001$ for cormorants and coots, respectively). Longer dives were more likely to be preceded by a leap rather than a surface dive (Fig. 1). Whitebreasted Cormorants also showed this pattern (Fig. 1) although while we were recording dive duration we never saw them perform full leaps. Crowned Cormorants always submerged using flat surface dives (Fig. 1). During 1984, just north of Saldanha Bay, we observed both Whitebreasted and Crowned Cormorants performing full leaps prior to submergence. Water depths at this time were 18 m and 11 m, respectively.

During our obervations of pursuit divers we never saw wing-propelled species engaging in pre-dive leaps, whereas most foot-propelled species did (Table 1).

DISCUSSION

In benthic foraging diving birds, dive duration is closely related to water depth (Dewar 1924, Cooper 1986, Wilson & Wilson 1988, Trayler *et al.* 1989, Wanless *et al.* 1991, Wanless & Harris 1991) because increased distance between the water's surface and the seabed necessitates increased transit time (Dewar 1924, Wilson & Wilson 1988).

The time used for transit is not directly profitable since it does not, in itself, yield food. In addition, the transit phase is energetically costly and limits the time available for searching for food on the bottom. It is thus in the best interests of diving birds to cover the transit phase as quickly and expending as little energy as possible (Lovvorn 1991, Wilson *et al.*

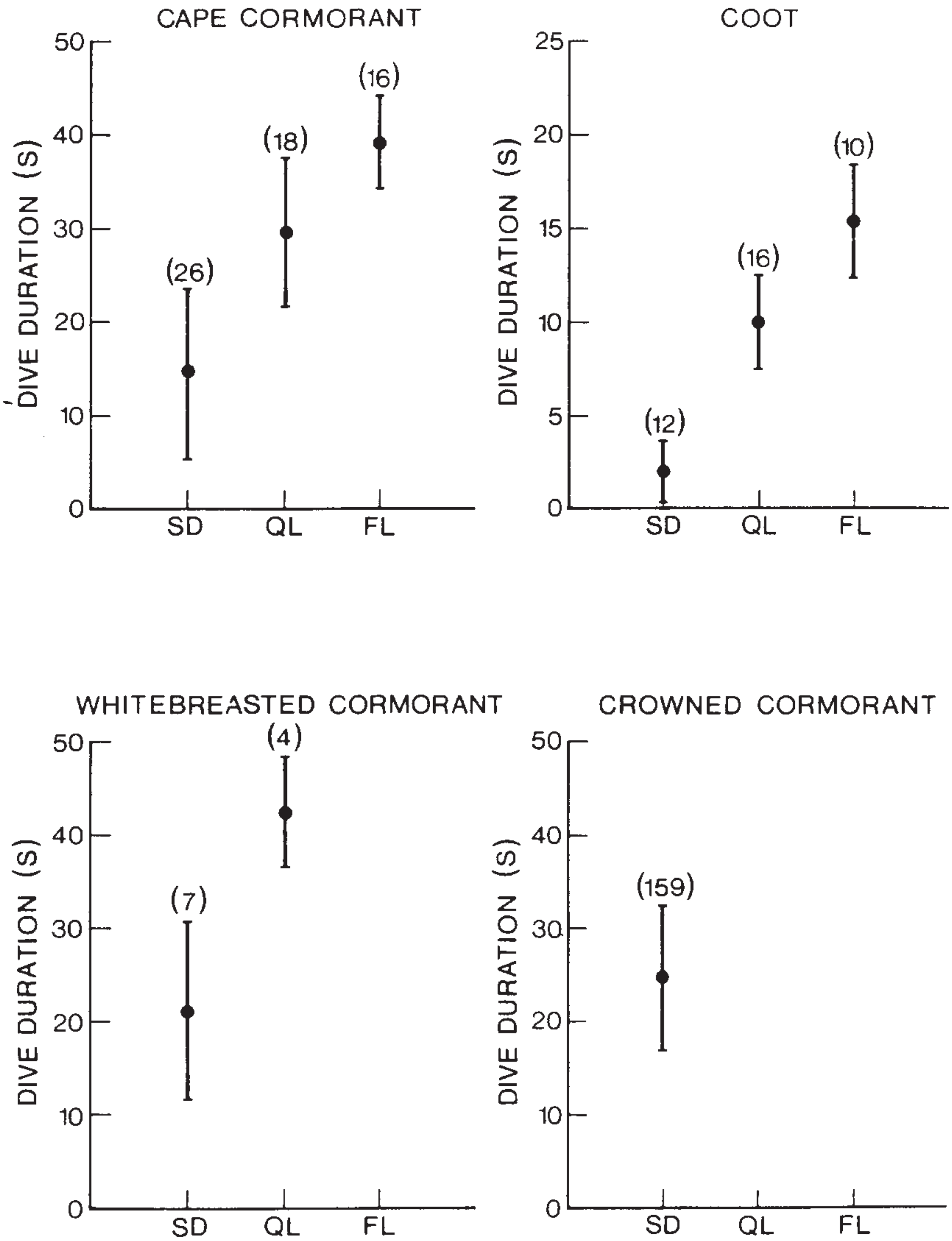

Figure 1

Relationship between dive duration and submergence technique in four species of diving birds foraging along the bottom. SD = surface dive, QL = quasi-leap, FL = full leap. Points denote means, vertical bars denote standard errors and the numbers in brackets indicate sample size.

TABLE 1

SPECIES OF DIVING BIRDS OBSERVED AND PRINCIPAL METHOD OF UNDERWATER PROPULSION IN RELATION TO WHETHER THE SPECIES HAS BEEN OBSERVED TO ENGAGE IN PRE-DIVE LEAPS

Species	N	Propulsion	Water >5m	depth <5m	Pre-dive leap
King Penguin *Aptenodytes patagonicus*	12	Wings	yes	yes	No
Gentoo Penguin *Pygoscelis papua*	24	Wings	yes	yes	No
Adelie Penguin *P. adeliae*	22	Wings	yes	yes	No
Chinstrap Pcenguin *P. antarctica*	36	Wings	yes	yes	No
Fiordland Crested Penguin *Eudyptes pachyrhynchus*	2	Wings	yes	yes	No
Rockhopper Penguin *E. chrysocome*	5	Wings	yes	yes	No
Macaroni Penguin *E. chrysolophus*	7	Wings	yes	yes	No
Yelloweyed Penguin *Megadyptes antipodes*	4	Wings	yes	yes	No
Little Penguin *Eudyptula minor*	20	Wings	yes	yes	No
Jackass Penguin *Spheniscus demersus*	71	Wings	yes	yes	No
Humboldt Penguin *S. humboldti*	17	Wings	yes	yes	No
Magellanic Penguin *S. magellanicus*	18	Wings	yes	yes	No
Redthroated Diver *Gavia stellata*	2	Feet	?	?	No
Great Northern Diver *G. immer*	1	Feet	yes		No
Little Grebe *Tachybaptus ruficollis*	12	Feet	?	?	Yes
Great Crested Grebe *Podiceps cristatus*	4	Feet	?	?	Yes
Common Diving Petrel *Pelecanoides urinatrix*	2	Wings	yes		No

Magellan Diving Petrel *P. magellani*	4	Wings	yes		No
Whitebreasted Cormorant *Phalacrocorax carbo*	24	Feet	yes		Yes
Cape Cormorant *P. capensis*	23	Feet	yes		Yes
Bank Cormorant *P. neglectus*	10	Feet	yes		Yes
European Shag *P. aristotelis*	3	Feet	yes		Yes
Rock Cormorant *P. magellanicus*	1	Feet		yes	No*
Imperial Cormorant *P. atriceps*	15	Feet	yes		Yes
Redlegged Cormorant *P. gaimardi*	1	Feet	yes		Yes
Spotted Cormorant *P. punctatus*	1	Feet		yes	No
Crowned Cormorant *P. coronatus*	11	Feet	yes		Yes
Razorbill *Alca torda*	4	Wings	yes		No
Guillemot *Uria aalge*	5	Wings	yes		No
Black Guillemot *Cepphus grylle*	8	Wings/feet	yes	yes	No
Pigeon Guillemot *C. columba*	8	Wings/feet	yes	yes	No
Marbled Murrelet *Brachyramphus marmoratus*	9	Wings	yes		No
Cassin's Auklet *Ptychoramphus aleuticus*	1	Wings	yes		No
Rhinoceros Auklet *Cerorhinca monocerata*	6	Wings	yes		No
Horned Puffin *Fratercula corniculata*	2	Wings	yes		No
Tufted Puffin *Lunda cirrhata*	2	Wings	yes		No
European Coot *Fulica atra*	10	Feet	yes		Yes

	Wing-propelled		Foot-propelled	
Pre-dive leap:	Yes	no	Yes	No
Total species:	0	23	11	3

* This species is documented as generally leaping in water deeper than 7 m by Wanless & Harris (1991).

TABLE 2

RELATIONSHIPS USED TO CALCULATE DIVE DEPTH FOR CORMORANTS FORAGING ALONG THE SEA BOTTOM IN SALDANHA BAY: D = WATER DEPTH (m), T = DIVE DURATION (s) (FROM WILSON & WILSON 1988). THESE RELATIONSHIPS ARE THEN USED TO DETERMINE THE DEPTH AT WHICH SPECIES ENGAGE IN SURFACE DIVES OR LEAPS. DIVE DURATION DATA IS DERIVED FROM FIGURE 1

Species:	Cape Cormorant	Crowned Cormorant	Whitebreasted Cormorant
	$T = 4.6D + 10$	$T = 5.4D + 6$	$T = 4.5D + 10$
Depth at surface dive:	1 m	3 m	2 m
Depth at quasi-leap:	4 m	?	7 m
Depth at full leap	6 m	?	?

1992). Pre-dive leaps are presumably adopted to achieve this. Correlations between the height of pre-dive leaps and dive duration, therefore, stem from correlations between the height of the leaps and water depth rather than to some correlation with duration *per se*.

We were unable to ascertain water depth directly during our study. However, Wilson & Wilson (1988) showed that there were very significant relationships between dive depth and dive duration for Cape, Crowned and Whitebreasted Cormorants foraging in Saldanha Bay. Dive duration increased linearly as a function of water depth for all three species. Regressions between dive depth and dive duration can thus be used to determine the depth of water in which the cormorants were executing surface dives and leaps. These relationships indicate that the Cape Cormorants that we observed began quasi-leaps at water depths between about 1 m and 4 m and that at a water depth of about 6 m the birds engaged in full pre-dive leaps (Table 2). Whitebreasted Cormorants began quasi-leaps at a water depth of between 2 m and 7 m.

From the above results we conclude the following:

(1) Foot-propelled divers are less likely to engage in pre-dive leaps as water depth decreases.

(2) Most foot-propelled divers do engage in pre-dive leaps in deep water although there are some exceptions.

(3) Wing-propelled divers do not engage in pre-dive leaps, irrespective of water depth.

Lovvorn (1991) documents the submergence techniques for a number of species of diving birds and considers, in particular, how birds overcome their buoyancy which is highest at the surface (Wilson *et al.* 1992). Lovvorn (1991) reports that divers *Gavia*, darters or anhingas *Anhinga*, Musk Ducks *Biziura lobata*, and grebes *Aechmophorus*, *Podiceps*, *Podilymbus* and *Tachybaptus* reduce buoyancy by lowering air-sac volumes and can execute flat-surface dives without apparent effort. Diving ducks of the genera *Aythya*, *Bucephala* and *Oxyura* engage in pre-dive leaps. Many grebes *Aechmophorus*, cormorants *Phalacrocorax*, mergansers *Mergus* and scoters *Melanitta* commonly also do this. Several sea ducks *Melanitta, Somateria* and *Histrionicus* and steamer ducks *Tachyeres* submerge by pulling themselves under with their wings. Guillemots *Cepphus* and Longtailed Ducks *Clangula hyemalis* submerge by wing action alone.

To determine possible reasons for the variation that we have observed, we must examine the forces acting on the bird when a dive is initiated.

Pre-dive leap

At the moment that a bird pushes against the water with its feet to leap into the air there is an upward force exerted which, when greater than the force exerted by gravity, accelerates the bird upward (Fig. 2a). Having left the surface of the water, the bird then decelerates due to gravity until its speed is zero. It then begins to accelerate back to the water. If the bird enters the water passively it is subject to an upward force from upthrust due to buoyancy and friction due to drag which results in deceleration (Fig. 2b). If, on entering the water, the bird actively swims it can exceed or equal these upward-acting forces to continue its descent (Fig. 2c).

Surface dive

If thrust is applied from the rear of the bird, downward force can be generated using movable anterior appendages such as the wings, head and neck as a hydrofoil. Overall, there is a horizontal force, opposed by drag and the force required for steering downward, and a vertical force, opposed by upthrust and drag (Fig. 2d). The more efficient the steering mechanism, the greater will be the downward vertical component compared to the horizontal component. The downward trajectory of the bird will be essentially curved and determined by these two components.

Vertial vs curved descent

For birds that feed on the seabed, vertical descents (Figs 2a, b, c) necessitate less energy utilized per metre depth of water than do curved descents (Fig. 2d) because there is no energy wasted creating a horizontal force.

Why do all birds not engage in vertical descents?

In order for a bird to be able to dive vertically it must orient its body vertically and be able to apply a downward force by thrusting with feet or wings. All seabirds are positively buoyant as a result of air trapped in the feathers (Wilson *et al.* 1992). In the extreme case, if a bird rotates about its lateral axis to up-end at the water's surface the wings are underwater but the feet are not. Thus, only wing-propelled divers can descend vertically from surface dives. Here, the speed of the descent is determined by the downward force applied by the bird. In order to descend as vertically as possible, foot-propelled divers must first leap out of the water so that they may gain enough momentum to immerse their body right up to their feet so that they can then begin thrusting. Pre-dive leaps are, however, clearly unsuitable for birds foraging in shallow water due to the danger of hitting the bottom at speed. Where water is shallow, foot-propelled divers must submerge using surface dives and incur the extra energetic cost of the horizontal force.

Descents close to vertical are only desirable in species wishing to feed on the sea bed in relatively deep water. Species feeding within the water column, e.g. most penguins, have shallow dive angles (unpubl. data for four penguin species). In addition, benthic divers feeding in shallow water, which travel horizontally along the bottom during normal prey searching, may descend at a shallow

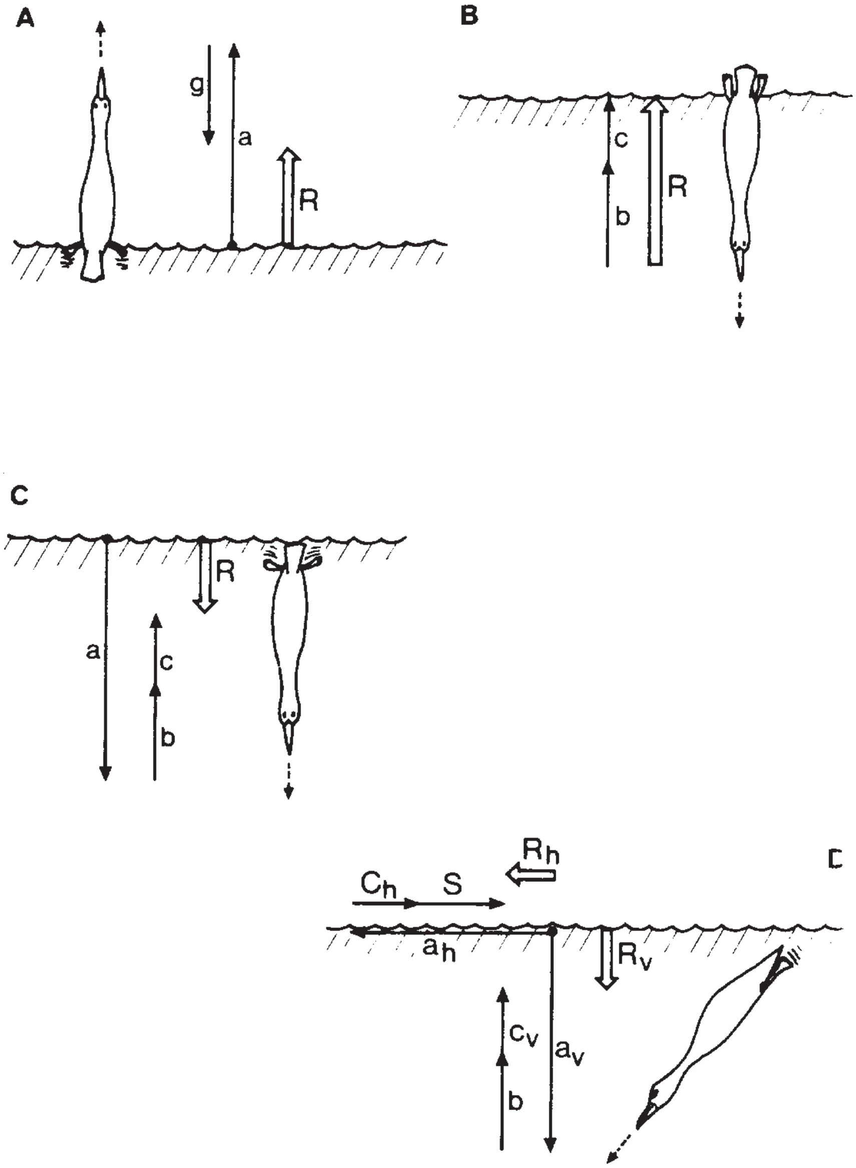

Figure 2

Simplified force diagram showing the principal forces acting on a seabird effecting submergence. The continuous lines with arrows denote forces and the dashed lines with arrows show the direction of motion. a = force applied by the bird by thrusting, b = force experienced from upthrust, c = drag, s = force applied as a result of steering, R = resultant force which leads to an acceleration or deceleration. Sub-scripts h and v denote horizontal or vertical components of forces where appropriate. The situations denoted are: (2a) Bird initiates a leap into the air from the surface of the water. (2b) Having executed the pre-dive leap the bird passively enters the water. (2c) Having executed the pre-dive leap the bird enters the water and immediately begins thrusting to dive deeper. (2d) Bird executes a surface dive.

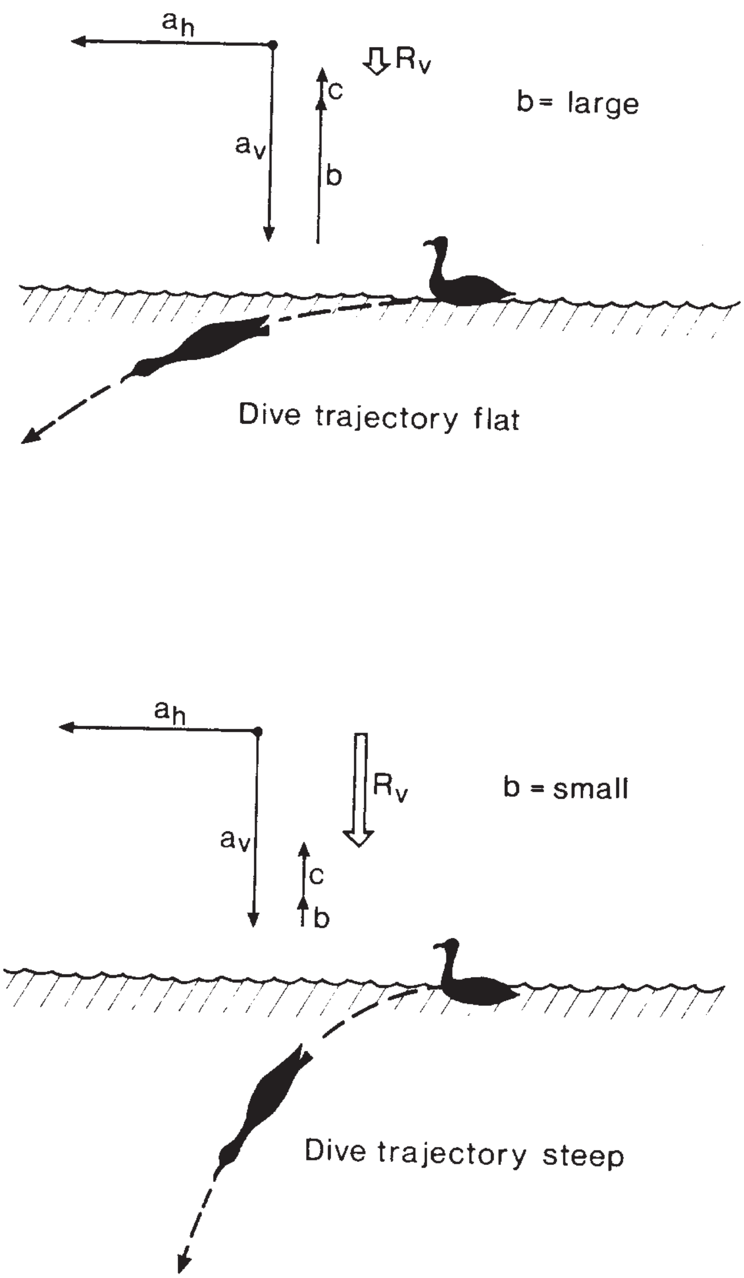

Figure 3

Simplified force diagram showing the change in resultant downward force when upthrust is large and small and the consequences this has for the dive trajectory. Terminology as in Fig. 2.

angle so as to avoid making an additional, unnecessary change in orientation. The benefits of travelling vertically presumably outweigh this disadvantage when feeding deep. Finally, leaps in relatively shallow water might startle potential prey and thus reduce feeding success.

Why do some foot-propelled divers not leap in deep water?

In addition to the efficiency of the steering mechanism, the rate at which a foot-propelled surface diver can descend the water column will depend greatly on the bird's buoyancy which determines the upthrust acting on the bird when submerged (Wilson *et al.* 1992). Highly buoyant species must use much of the downward thrust exerted by the legs simply to counteract the high upthrust, which leaves little resultant force for downward movement. The horizontal component of the movement is thus relatively greater which means that the dive trajectory is flat and the descent rate low (Fig. 3a). Conversely, as the upthrust tends towards zero, so the dive trajectory becomes steeper with the bird descending the water column faster and with less energy (Fig. 3b). Thus, foot-propelled diving birds with little air in the feathers which reduces the upthrust, such as divers *Gavia* (Wilson *et al.* 1992), may descend the water column fast and efficiently from surface dives (Lovvorn 1991). Dives for such species may be particularly advantageous when foraging in water of highly variable depth.

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