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# CENTRO DE INVESTIGACIÓN CIENTÍFICA Y DE EDUCACIÓN SUPERIOR DE ENSENADA

## PROGRAMA DE POSGRADO EN CIENCIAS EN ECOLOGÍA MARINA

## BIOMECHANICAL CONFLICTS BETWEEN DIVING AND AERIAL FLIGHT DUE TO PLUMAGE WETTABILITY OF *Oceanodroma leucorhoa*, *Synthliboramphus hypoleucus* AND *Ptychoramphus aleuticus*

TESIS

que para cubrir parcialmente los requisitos necesarios para obtener el grado de
DOCTOR EN CIENCIAS

Presenta:

VÍCTOR MANUEL ORTEGA JIMÉNEZ

Ensenada, Baja California, México, agosto de 2009.

**ABSTRACT** of the thesis presented by **Víctor Manuel Ortega-Jiménez** as a partial requirement to obtain the DOCTOR OF SCIENCE degree in Marine Ecology. Ensenada, Baja California, México. August 2009.

**BIOMECHANICAL CONFLICTS BETWEEN DIVING AND AERIAL FLIGHT DUE TO PLUMAGE WETTABILITY OF** *Oceanodroma leucorhoa, Synthliboramphus hypoleucus* **AND** *Ptychoramphus aleuticus***.**

Seabirds face unique tradeoffs between flying and diving, which are generally resolved according to their marine habitats and distinctive foraging modes. These tradeoffs are perhaps most pronounced in diving birds, which must not only contend with conflicting evolutionary pressures associated with flying but also with underwater swimming. Plumage wettability is an important factor in these tradeoffs as birds make transitions from air to water and *vice versa*. Dry plumage, which depends of feather microstructure, improves flying ability but increases buoyancy, which is a detriment to diving. The properties of wet feathers, and the effects of plumage wettability in flight and diving performance were analyzed in three seabird species: two wing propelled divers with high wing loading, Cassin's Auklet (*Ptychoramphus aleuticus*) and Xantus's Murrelet (*Synthliboramphus hypoleucus*); and Leach's Storm-petrel (*Oceanodroma leucorhoa*), a surface feeder with low wing loading. I approached this issue by determining the mechanical costs of plumage wettability in takeoff and diving, both non-stationary modes of locomotion. Dry feathers did not resist any pressure for air penetration, but one-side wet feathers of both alcids resisted a critical air pressure of 1.25 kPa. Water pressure resistance of one-side wet feathers was 1.44 kPa for Xantus's Murrelet and 1.36 kPa for Cassin's Auklet. These results suggest that plumages with wet appearance reduce body heat loss during emersions after diving without losing their resistance to water penetration. Plumage wettability effect on takeoff performance was evaluated. The plumage of alcids held less water than that of the Storm-petrel (~6.7% of body mass *vs*. 9.5%). Examination of takeoff performance, both before and after experimentally submerging the birds, indicated that wingbeat frequency, speed and mass-specific power (peak and mean), and energy per wingbeat decreased in all species when plumage was experimentally wetted; whereas, mean acceleration increased. Leach's Storm-petrel was more strongly affected by wet plumage than the alcids, with a 32% reduction in mass specific energy per wingbeat compared to ≤25% in the alcids. Takeoff angle was reduced in alcids, but not significantly so in *O. leucorhoa*. Mean maximum extra load supported by Leach's storm petrels was 45% of body mass, 23% by Cassin's Auklet, and 21% by Xantus's Murrelet. Mean maximum induced power output was 0.7 W for Leach's Storm-petrel, 4.5 W for Cassin's Auklet, and 5.7 W for Xantus's Murrelet. Diving performance was tested increasing experimentally the air volume (16% of the original content with a low density polyethylene vest) of Cassin's Auklet and Xantus's Murrelet, compared with two control groups (one non-manipulated and one with a neutral buoyancy vest). Also, the loss of air, as bubbles, with time was measured. Manipulated birds, loaded with an artificial air vest, reduced their descent speed, distance per flap, and work per flap compared with non-manipulated birds of both alcids. Significant differences were found in the flap duration of auklets only. In contrast, no difference was found in the loss of air volume and the cost of transport between experimental groups of both alcids. Non-manipulated birds presented a higher drag than buoyancy; meanwhile the contrary was found for manipulated birds. The air volume loss by Cassin's Auklet and Xantus's Murrelet measured during divings down to 0.7 m depth was 9% and 8% of the total air volume, respectively.

**Key words:** seabirds, feather structure, wettability, takeoff performance, *Oceanodroma leucorhoa, Ptychoramphus aleuticus, Synthliboramphus hypoleucus*.

**RESUMEN** de la tesis de **Víctor Manuel Ortega Jiménez,** presentada como requisito parcial para la obtención del grado de DOCTOR EN CIENCIAS en Ecología Marina. Ensenada, Baja California. Agosto 2009.

**CONFLICTOS AERODINÁMICOS Y DE BUCEO POR ADHESIÓN DE AGUA AL PLUMAJE EN** *Oceanodroma leucorhoa***,** *Synthliboramphus hypoleucus* **Y** *Ptychoramphus aleuticus***.**

Resumen aprobado por:

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Saúl Álvarez Borrego
Director de Tesis

Las aves marinas enfrentan compromisos únicos con relación a la cantidad de agua absorbida por el plumaje y las habilidades tanto de vuelo como de buceo debido a las restricciones impuestas por el hábitat marino y sus historias de vida. En el presente estudio se analizan las propiedades estructurales de las plumas y los efectos mecánicos de despegue y buceo asociados al agua adherida al plumaje de tres especies de aves marinas: dos aves que bucean usando las alas y con carga alar grande, *Ptychoramphus aleuticus* y *Synthliboramphus hypoleucus*; y una especie que forrajea en la superficie del mar, con carga alar baja, *Oceanodroma leucorhoa* (incluida sólo en la parte del vuelo). Se encontró que las plumas mojadas ventralmente de los dos álcidos resisten una presión de aire máxima de 1.25 kPa. Las plumas de *S. hypoleucus* resistieron una presión de penetración de agua de 1.44 kPa, mientras que para *P. aleuticus* resistieron 1.36 kPa. Se evaluó el efecto del agua en el plumaje con relación a la habilidad de despegue de *S. hypoleucus, P. aleuticus* y *O. leucorhoa*. El plumaje de los álcidos retuvo menos agua que el de *O. leucorhoa* (~6.7% de la masa del cuerpo $m_b$ vs. 9.5%). La evaluación del despegue de estas tres especies, antes y después de mojar experimentalmente el plumaje, indica una reducción en la frecuencia de aleteo, velocidad, potencia por unidad de masa (media y máxima), energía mecánica por aleteo, pero un aumento en la aceleración. Durante el despegue, *O. leucorhoa* redujo su energía por unidad de masa y por aleteo en un 32%, mientras que para los álcidos fue ≤25%. El ángulo de despegue se redujo en los álcidos, pero no en *O. leucorhoa*. Los experimentos de carga máxima indican que *O. leucorhoa* soportó, con relación a $m_b$, una carga extra del 45%, mientras tanto para *P. aleuticus* fue 23% y para *S. hypoleucus* fue 21%. La potencia máxima inducida fue 0.7 W para *O. leucorhoa*, 4.5 W para *P. aleuticus* y 5.7 W para *S. hypoleucus*. La habilidad de buceo fue evaluada incrementando experimentalmente el volumen de aire en los dos álcidos (16% más del contenido de aire original con un chaleco de polietileno de baja densidad)*,* y se comparó con dos grupos control (sin carga y con un chaleco con flotabilidad neutra). Además, se cuantificó la pérdida de aire (burbujas) con respecto al tiempo. En ambas especies, los especimenes manipulados redujeron su velocidad de descenso, distancia y trabajo por aleteo en comparación con los controles. En *P. aleuticus* hubo diferencias significativas en el período de aleteo. En ambas especies no hubo ningún efecto en la pérdida de volumen de aire y en el costo de transporte entre grupos experimentales. Mientras que en las aves manipuladas fue al revés. El volumen de aire perdido por *P. aleuticus* y *S. hypoleucus* fue respectivamente de 9% y 8% del contenido original, durante el buceo a 0.7 m de profundidad*.*

**Palabras Clave:** Aves marinas, despegue, buceo, agua en el plumaje, *Oceanodroma leucorhoa, Synthliboramphus hypoleucus* y *Ptychoramphus aleuticus*.

# Dedicatoria

A mi familia, especialmente a ti, Sarahí, mi más valioso y sutil descubrimiento.

## Acknowledgments

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**Chapter I**

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**Plumage wettability and seabirds locomotion**

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## I.1 General Introduction

Seabirds invest most of their lifespan on water and they are dependent upon an insulating layer of air within the plumage for effective thermoregulation (Stephenson, 1994). Waterproofing and resistance to water penetration of plumage are a consequence of feather microstructure (Rijke, 1970). Paradoxically some seabirds show a 'wet' appearance after successive dives indicating that their plumage has a poor capacity to repel water, but their plumage is still effective in preventing water penetration (Grémillet et al., 2005; Ribak et al., 2005). Studies indicate that water retained in the plumage can amount to as much as 10% of body mass in seabirds (Mahoney, 1984; Ortega-Jiménez et al., 2009). Thus, wet birds are heavier, with increased wing loading and energetic costs associated with flying (Pennycuick, 1978). However, birds generally shed water from their plumage as they fly, which would indicate that the negative effects of wet plumage are most important during takeoff.

Takeoff uses about four times the mass-specific mechanical power of cruising flight (Askew et al., 2001). Water absorbed by the plumage effectively increases wing loading, which decreases aerodynamic efficiency, and increases the induced power requirements for flight, which is the cost of lift production (Pennycuick, 1975). Additionally, water retained by the wing feathers could affect the moment of inertia during flapping, causing increased inertial power during the initial flap cycles of takeoff (Van den Berg and Rayner, 1995). Leg thrust, when employed in conjunction with wing flapping, reduces the demand on flight muscle power during takeoff, helping to maximize initial flight velocity (Earls, 2000;

Tobalske et al., 2004). However, birds floating on the water cannot use leg thrust as effectively as birds on solid ground, which means that the wings must bear more of the burden for at-sea takeoffs (Norberg and Norberg, 1971). Hence, the negative effects of wet plumage on takeoff performance may be especially critical for seabirds. Nevertheless, there have been no detailed kinematic studies to quantify the effects of wet plumage on takeoff performance.

Flying animals require relatively high capacity for power and lift production to become airborne (Askew et al., 2001). The maximum load supported during short-bursts in flying animals seems to be positively correlated with muscle mass (Marden, 1987; 1990). Marden (1990) suggested that maximum induced power output can be predicted using the actuator-disk equation for hovering flight (Weis-Fogh, 1972). Due to these takeoff limitations, plumage wettability could restrict the capacity to carry food to chicks during the reproductive season.

Diving birds that forage in shallow waters need to overcome buoyancy that is the main component for mechanic costs (Lovvorn and Jones, 1994). Buoyancy is not only reduced with increasing depth as a consequence of Boyle's law (Wilson et al., 1992), but also by losses of air from plumage and/or respiratory system. In Lesser Scaup *Aythya affinis* compression due to hydrostatic pressure and the loss of air from plumage decrease buoyancy by 32% of original air volume in the body (Stephenson, 1994). Moreover, it has been suggested in cormorants that plumage wettability (up to 6% of body mass) could reduce the air content in plumage, reducing buoyancy by 18% (Ribak et al., 2005). On the other hand, air from the respiratory system could be reduced in a bird making dives following exhalation, as has been observed in great cormorants and some ducks (Ross, 1976; Tome and Wrubleski, 1988). Also, shallow diving penguins exhibit a reduced air volume in their respiratory system to avoid high buoyancy costs (Sato et al., 2002; 2006).

Theoretically, speed should to be affected by buoyancy changes due to hydrostatic pressure. Lovvorn et al. (1999) developed a biomechanical model assuming that the stroke frequency and the work per flap stay constant as buoyancy changes with depth. These kinds of models predict a gradual increase of speed with depth to an asymptotic maximal. However, empirical data show that medium size alcids maintain a relatively constant swimming speed

during descent (Lovvorn et al., 1999; Watanuki et al., 2006). Lovvorn et al.'s (1999) model failed to predict the observed diving speed, perhaps because it does not take into account air losses from plumage and respiratory system during the first meters of the descent. It is possible to reach close to maximal speed rapidly when taking into consideration these air losses.

Three small size seabird species were selected for this study: *Ptychoramphus aleuticus* (Alcidae; Pallas, 1811) and *Synthliboramphus hypoleucus* (Alcidae; Xantus de Vesey, 1860) are alcids, diving birds with relatively high wing loading and high flight costs (Roby and Ricklefs, 1986; Hodum, 1998). *Oceanodroma leucorhoa* (Hydrobatidae; Vieillot, 1818) is a sea-surface feeder with low wing loading and low flight costs, which rarely dives below the water surface (Manuwal, 1974; Murray et al., 1983; Huntington et al., 1996).

Chapters were written as a collection of individual papers, thus material repetitions were unavoidable. Chapter two describes an examination of water and air penetration in wet and dry feathers of Cassin's Auklet and Xantus's Murrelet. Chapter three examines and compares the effects of plumage wettability on takeoff performance of Cassin's Auklet, Xantus's Murrelet and Leach's Storm-petrel. Chapter four describe an evaluation of the maximal load-lift production and induced power output performed by Cassin's Auklet, Xantus's Murrelet and Leach's Storm-petrel. Chapter five examines and compares the effects of air content changes on diving performance of Cassin's Auklet and Xantus's Murrelet. Chapter six discusses future work derived from the present study. Finally, Chapter seven presents the main conclusions arising from this thesis.

## I.2 Objectives

- To describe and compare feather structure of *P. aleuticus, S. hypoleucus,* and *O. leucorhoa.*

- To measure maximal pressure resistance of water and air of feathers of both alcids.

- To measure and compare water absorption of plumage of *P. aleuticus, S. hypoleucus,* and *O. leucorhoa.*

- To measure the effects of plumage wettability on takeoff performance of *P. aleuticus, S. hypoleucus,* and *O. leucorhoa.*

- To measure maximum load supported during takeoff of *P. aleuticus, S. hypoleucus,* and *O. leucorhoa.*

- To measure the effects of buoyancy decrement, due to hydrostatic pressure and loss of air from plumage and/or respiratory system, in diving performance of *P. aleuticus, and S. hypoleucus.*

## I.3 Hypotheses

- Alcids present a wet 'appearance' after diving, but inside their plumage remains dry. Thus, wet feathers, despite their failure to completely repel water, must resist water and air penetration pressure (like a wet paper).

$$H_o: \mu_w = \mu_D$$
$$H_1: \mu_w \neq \mu_D,$$

where $\mu_w$ is the average of maximal pressure resistance to water penetration when the feather was wet on one side, and $\mu_D$ is the same for dry feathers.

- Due to differences in life histories and locomotion, it is expected that the Storm-petrel retains more water than the alcids. But, no differences are expected between the two alcids.

$$H_o: \mu_{sp} = \mu_{a1} = \mu_{a2}$$

$$H_1: \mu_{sp} \neq \mu_{a1} = \mu_{a2},$$

where $\mu_{sp}$ is the average of the amount of water retained by the Storm-petrel, $\mu_{a1}$ and $\mu_{a2}$ are the same for the two alcids.

- Afterfeather:feather length ratio is significantly different between all three species.

$$H_o: \mu_{sr} = \mu_{ar1} = \mu_{ar2}$$

$$H_1: \mu_{sr} \neq \mu_{ar1} = \mu_{ar2},$$

where $\mu_{sr}$ is the average of the afterfeather:feather length ratio of the Storm-petrel, and $\mu_{ar}$ and $\mu_{ar}$ are the same for the two alcids.

- Given that wet plumage causes an increase in body mass, aerodynamic theory predicts decreases in takeoff angle, maximal acceleration, maximal speed and peak power for all species when the plumage is wet. Similarly, a decrease of wingbeat frequency is predicted.

$$H_o: \mu_{ktw} = \mu_{ktD}$$

$$H_1: \mu_{ktw} \leq \mu_{ktD},$$

where $\mu_{ktw}$ is the average of each mechanical takeoff variable of wet birds and $\mu_{ktD}$ are the same for dry birds.

- In agreement with hydrodynamics, it is expected that speed is affected positively by buoyancy reduction during descending diving.

$$H_o: \mu_{uhb} = \mu_{ulb}$$

$$H_1: \mu_{uhb} \geq \mu_{ulb},$$

where $\mu_{uhb}$ is the average of the diving descent speed of manipulated birds with high mass specific buoyancy and $\mu_{ulb}$ is the same for non-manipulated birds.

## I.4 Study site and species

The study site was located at West San Benito Island (28°18' N, 115°34' W), off the west coast of central Baja California. This island is close to the southern limit of each of the three species' breeding range. Data collection was carried out from 3 April through 28 May

2007. Mean air temperature $T_c$ at night was 11˚C (ranging from 7˚C to 13˚C); mean air pressure $P_{atm}$ at sea level was 1008.8 hPa. The calculated air density $\rho_a$ was 1.234 kg m$^{-3}$ ($\rho_{a\ =}\ P_{atm}\ /\ [R\ T_c]$, where $R$ is the gas constant 287.05 J kg$^{-1}$ ˚K$^{-1}$, note that $T_c$ must be in Kelvin).
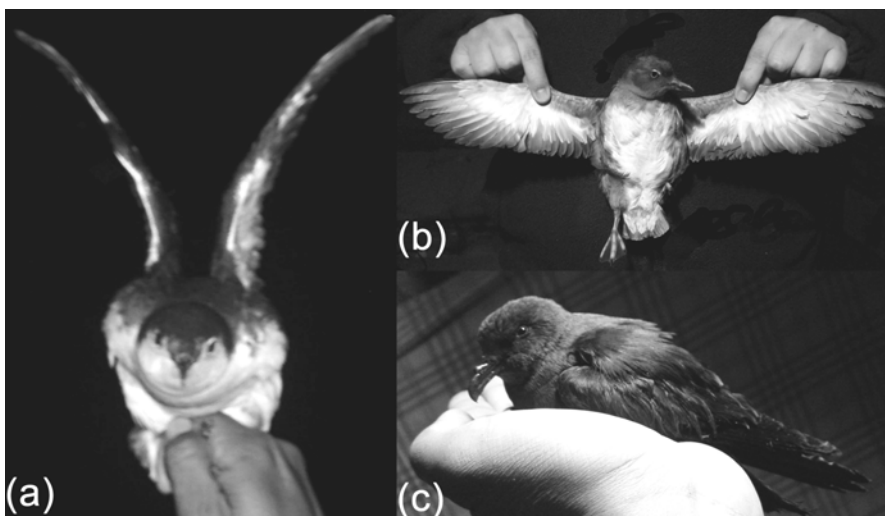


**Figure 1. Study species. (a) Xantus's Murrelet. (b) Cassin's Auklet. (c) Leach's Storm-petrel. Figura 1. Aves marinas. (a) *S. hypoleucus*. (b) *P. aleuticus*. (c) *O. leucorhoa*.**

The three seabird species studied present biological and biomechanical differences in many respects (Fig. 1). Cassin's Auklet and Xantus's Murrelet are members of the Alcidae family. Both species are wing-propelled divers with high wing loading. But, auklets have larger legs and shorter pelvic bones than those of murrelets (Storer, 1945). During the reproductive season, adults select a nest from burrows, rock crevices or under vegetation on coastal slopes of the island. Chick development differs between both alcids. Chicks of Xantus's Murrelet leave their nests two days after hatching and go to the sea, while chicks of Cassin's Auklet stay in their nests until growing up to 90% of their adult mass (Manuwal, 1974; Murray et al., 1983). On the other hand, Leach's Storm-petrel is one of the most common procellariiform breeding in the Northern hemisphere. It is highly pelagic and during the breeding season it returns to land at night. It has a small wing loading. At sea, Leach's Storm-petrel is an opportunistic surface feeder and it is known to forage on a variety of plankton and nekton at or near the sea surface (Huntington et al., 1996).

# Chapter II

## Effect of wetting single feathers on air outflow and on resistance to water penetration

## II.1 Abstract

The wet appearance of small size alcids after diving suggests that their feathers have poor water repellency. Paradoxically, once wet, their plumage resists water penetration effectively. This study's objective was to evaluate the effect of feather wetting on the critical penetration pressure of air (maximum pressure for resistance to air penetration, $P_a$) and water ($P_w$). $P_a$ was measured in contour feathers of Xantus's Murrelet (*Synthliboramphus hypoleucus*) and Cassin's Auklets (*Ptychoramphus aleuticus*) under two conditions: dry (feathers with separated barbs) and one-side wet (feathers with aggregated barbs). Dry feathers did not resist any pressure for air penetration, but one-side wet feathers of both alcids resisted 1.25 kPa. $P_w$ for Xantus's Murrelet was 1.44 kPa, and it was 1.36 kPa for Cassin's Auklet. These results suggest that plumages that have wet appearance reduce body heat loss (warm air loss from plumage) during emersions after diving without losing their resistance to water penetration.

## II.2 Resumen

Algunas especies de aves marinas, como los álcidos, muestran una apariencia mojada después de bucear. Paradójicamente, la exploración de la parte interna de su plumaje indica que se encuentra seca. Con el fin de entender los efectos debidos a la adhesión superficial de agua en las plumas con relación a la resistencia a la penetración de agua ($P_w$) y aire ($P_a$), se hicieron mediciones en plumas individuales del pecho de *S. hypoleucus* y *P. aleuticus* bajo dos condiciones: secas (plumas con barbas separadas) y mojadas dorsalmente (plumas con barbas agregadas). Se encontró que las plumas mojadas dorsalmente de ambos álcidos resisten efectivamente una presión máxima de aire de 1.25 kPa. Sin embargo, la resistencia máxima de penetración de agua no difirió significativamente entre plumas mojadas ventralmente y plumas secas. $P_w$ para *S. hypoleucus* fue de 1.47 kPa y para *P. aleuticus* fue 1.36 kPa. Estos resultados sugieren que el plumaje aparentemente mojado, de ambos álcidos, impide la pérdida de aire caliente durante las sucesivas emersiones de buceo, reduciendo los costos por pérdida de calor corporal.

## II.3 Introduction

Stephenson and Andrews (1997) suggested that feathers of aquatic birds must be highly water repellent to prevent the displacement of the internal air layer and to avoid an excessive heat loss. Ducks and some aquatic species (dippers, loons, and grebes) have feathers with highest capacity to repel water (Rijke, 1970). Nevertheless, some seabirds show a wet appearance after successive divings giving the impression of a poor waterproof capacity to an observer from afar. The Cassie-Baxter model predicts that feathers with poor water repellency have a good resistance to water penetration (Rijke, 1970), which seems to be paradoxical. Thus, wet appearance of plumage does not necessarily imply excessive heat loss, as the insulating layer of the plumage is not compromised. However, wet birds are

heavier, with increased wing loading and energetic costs associated with flying. Ortega-Jiménez et al. (2009) showed that plumage wettability had a negative effect on takeoff performance of alcids. Then, the role of an apparently 'wet' plumage remains to be explained (Fig. 2).



**Figure 2. Xantus's Murrelet 'wet' after a prolonged set of divings inside a tank.**
**Figura 2.** *S. hypoleucus* **mojado aparentemente después de bucear dentro de un tanque experimental.**

Alcids could be viewed as intermediate between the 'dry-plumage' birds and cormorants, which get completely soaked when diving (Mahoney 1985; Ribak et al., 2005). Possibly, alcids have resolved the costs and benefits of flight, diving and heat maintenance by attaining intermediate wetting.

In order to evaluate the hypothesis that apparent wet plumage of alcids impedes water penetration and warm-air outflow during bird emersion, after diving, we measured air and water maximum penetration pressure of one-side wet feathers. Feathers of Xantus's Murrelet (*Synthliboramphus hypoleucus*) and Cassin's Auklets (*Ptychoramphus aleuticus*) were used.

## II.4 Methods

### II.4.1 Water pressure resistance

Feathers were collected from a specimen of each one of the two alcids on San Benito Island, Baja California, in the coastal California Current System. The afterfeathers were removed before running the experiments. Critical penetration pressure ($P_w$) was defined as the hydrostatic pressure required for water to start penetrating through a single feather, and it was measured following Stephenson and Andrews (1997). The dorsal part of each single feather was fixed downwards with Loctite on a test tube (3mm internal diameter, 4 cm length). The test tube was connected to the lower part of a large J-shaped plastic tube. The upper part of the J tube (6mm internal diameter) was then progressively filled with water so that the dorsal surface of the feather would suffer an increasing pressure, until the water started penetrating through the feather.
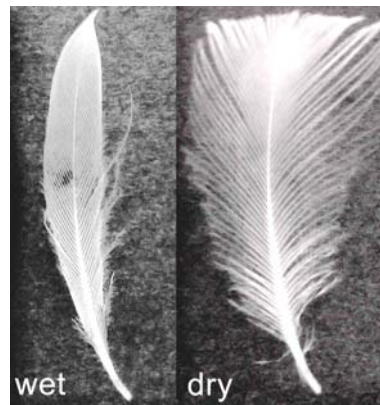


**Figure 3. Xantus's Murrelet's breast feathers under dry and one-side wet conditions.**
**Figura 3. Plumas del pecho de *S. hypoleucus* bajo dos condiciones: seca y mojada ventralmente.**

This procedure was performed in two fashions. In one case the feather was originally dry and fixed to the test tube. This treatment was made to compare with other studies (Stephenson and Andrews, 1997; Grémillet et al., 2005). In the second case the feather was one-side wetted previous to its attachment to the test tube. To do this, the feather was placed dorsally on water, holding it at the rachis with the fingers and pushing it lightly into

the liquid surface without submerging it completely. The result of this procedure was a feather with aggregated barbs, with a dry ventral side and a wet dorsal side (one-side wet) (Fig. 3). The one-side wet feather was placed dorsally for ~2 s on a paper napkin, to remove excess water. Care was taken that the feather preserved the aggregated barbs structure, and then it was fixed to the test tube.

## II.4.2 Air pressure resistance

An air manometer was constructed to measure resistance to maximal air pressure ($P_a$). The apparatus used the principle of communicating vessels. A single feather was fixed between two plastic tubes (3mm internal diameter) using a mechanical press and this arrangement was connected to a bottle half-filled with water. This connection was made to the air in the bottle. A manual air pump was connected to the air in the bottle to be able to change its pressure. A tube was inserted vertically into the bottle down to the water. If pressure is increased in the inner air, both the water level of the vertical tube and the air pressure resisted by the sample feather increase (Fig. 4). The air pump was used to progressively increase inner pressure until the water level of the vertical tube reached its maximal height and dropped-off rapidly. The maximal water height was then transformed to estimate the exerted pressure $P_a$ ($P_a = \rho g h$, where $\rho$ is water density, $g$ is gravity acceleration, and $h$ is the maximal water height; a correction for capillarity was done to $h$ subtracting 2.6 mm). Measurements were made with dry and one-side wet feathers. For one-side wet feathers, a procedure similar to the one for measuring $P_w$ was followed.
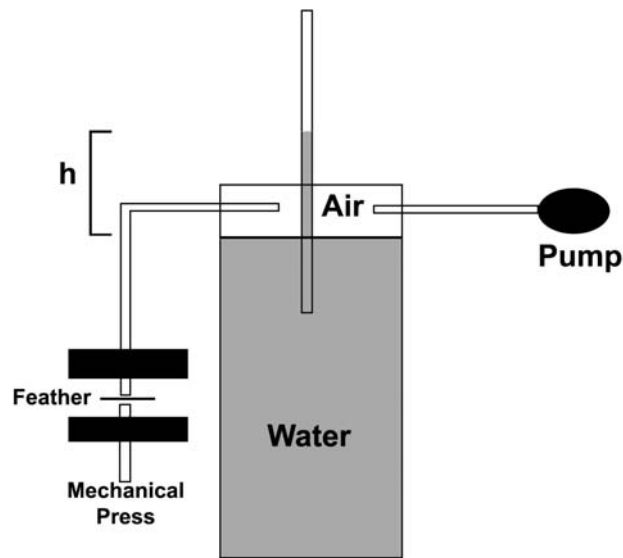
**Figure 4. Manometer used to measure the critical pressure of air through a single feather.**
**Figura 4. Dispositivo utilizado para medir la presión crítica de resistencia a la penetración de aire en plumas individuales.**

### II.4.3 Statistical Analyses

Thirty ventral feathers of each of the two species were used to measure the two variables ($P_w$ and $P_a$), fifteen for each condition (dry and one-side wet). Independent-samples *t*-tests (SPSS v.12) were used to compare means of variables between conditions. In all statistical analyses, the probability level at which the null hypotheses of 'no difference' were rejected was $p>0.05$. In what follows, data are shown as mean ± standard error.

## II.5 Results

In the central part of the feather, barbules run perpendicular to the barbs. Close to their attachment, they have a blade-like structure, but at their distal part they are plumulaceus. SEM images show that, after one-side wetting, the plumulaceus part of the barbules aggregates and compacts more than the blade-like structure. Also, barbs at the pennaceous part of the feather aggregate with wetting (Fig 5).
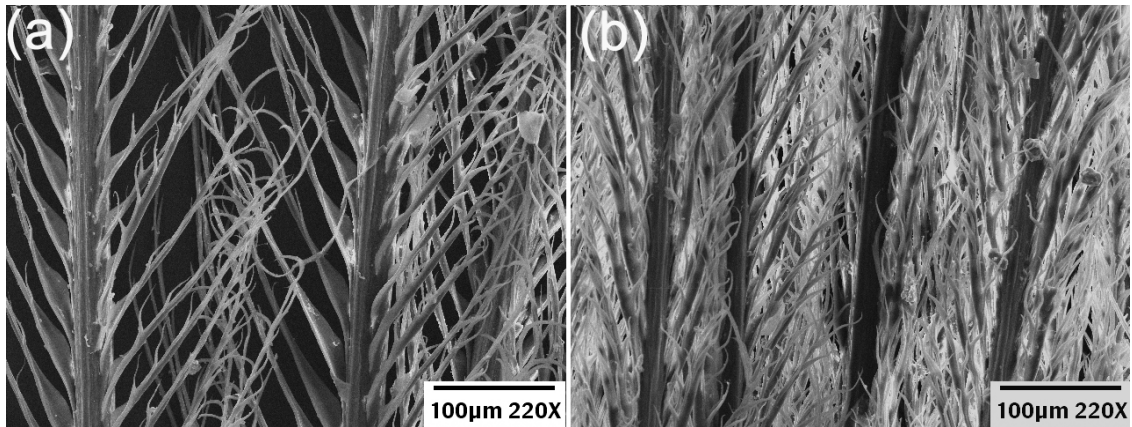
**Figure 5. Scanning Electron Microscope images of the pennaceous barbs of a Xantus's Murrelet feather: (a) Dry feather; (b) One-side wet feather.**
**Figura 5. Imágenes de microscopio electrónico de barrido de las barbas del penacho de la pluma de *S. hypoleucus*: (a) Pluma seca; (b) Pluma mojada ventralmente.**

$P_w$ for feathers with spaced (dry) barbs did not differ significantly from that for aggregated (one-side wet) barbs (murrelet: $t_{14}$ = 0.938, $p$ = 0.356; auklet: $t_{14}$ = 0.253, $p$ = 0.802). Average $P_w$ of feathers with spaced and aggregated barbs was 1.47 ± 0.025 kPa and 1.44 ± 0.027 kPa for Xantus's Murrelet, respectively; and 1.37± 0.022 kPa and 1.36 ± 0.028 kPa for Cassin's Auklet, respectively.

$P_a$ experiments indicated that dry feathers are totally permeable to air ($P_a$ is atmospheric pressure). But, when feathers were one-side wet, air pressure was resisted effectively up to a maximum. $P_a$ for wet feathers of murrelets was 1.27 ± 0.042 kPa, and it was 1.23 ± 0.037 kPa for auklets.

## II.6 Discussion

### II.6.1 Feather wetting

In order to explain the capacity of feathers to retain water and avoid heat loss it maybe helpful to attend to water repellency theories for textiles. The Cassie-Baxter model indicates that air can remain trapped below a water drop forming 'air pockets', thus strengthening water repellency of porous material. This is because the drop sits partially on

air, increasing the apparent contact angle in agreement with the Young equation (Cassie and Baxter, 1944). Water repellency also could be explained with the Wenzel model, which indicates that material roughness increases the surface area of the solid, geometrically enhancing hydrophobicity. Nevertheless, Wenzel model predicts an increase of hidrophilicity if porous material is hydrophilic. Bormashenko et al. (2007) found that the tissue forming the feather is hydrophilic. Thus, a wetting transition from waterproof capacity to totally wetting of bird feathers is to be expected. A Cassie–Wenzel transition may occur on pigeon feathers and rough materials when the radius of an evaporating drop decreases, or by increasing external pressure on the drop (Lafuma and Quéré, 2003, Bormashenko et al., 2007). A particularity of the Wenzel regime is that it produces a stronger adhesion of a drop on the surface of rough materials than that of the Cassie regime (Lafuma and Quéré, 2003). Thus, the Wenzel model could explain the one-side wet feather condition.

**II.6.3 Water pressure resistance**

Rijke's (1970) theoretical results suggested that feathers of aquatic birds, like those of alcids, may be only marginally resistant to water penetration. However, our results indicate that single feathers of both alcids effectively resist water penetration when they have either spaced or aggregated barbs. Stephenson (1997) did not find differences of water pressure resistance between 'dry' feathers and feathers held in prolonged contact with water at a pressure similar to that exerted at the ventral part of a floating Lesser Scaup. Other studies indicate that 'dry' feathers of diving birds resist higher water pressure than that predicted by Rijke (1970) (Stephenson and Andrews, 1997; Grémillet et al., 2005; Bakken et al., 2006). Our results support the hypothesis that plumage of aquatic birds are resistant to water penetration, even when they sit on the water for long times. The $P_w$ values for both alcids may be explained in part by the loose irregular structure of barbs and barbules of their feathers (Fig 3). Grémillet et al. (2005) found that body feathers of cormorants are partially wettable because they have a loose outer section and highly waterproof central portion.

## II.6.2 Air pressure resistance

Our average $P_a$ for one-side wet feathers agrees with the observations made for wet paper. In the latter, with ~85% water content or more, no air intrusion occurs at low air pressures (Van de Ven, 2008). But, in contrast with the fibers of wet paper, feather wetting induces barbs to clump together effectively reducing the exposure area and increasing capillary forces. Studies of the elastocapillary coalescence in wet hair indicate that pairs of bundles aggregate successively, forming complex hierarchical patterns that depend on a balance between capillary forces and the elasticity of the lamellae (Bico et al., 2004). Ventral feathers of both alcids present an entire vane with a loose irregular structure (Ortega-Jiménez et al., 2009). Thus, capillary forces and elasticity in part explain barb aggregation of one-side wet feathers.

$P_a$ for both alcids predicts no air outflow from plumage when a seabird is floating on the sea surface. However, this result must be applied with caution to explain air losses observed in auklets and murrelets when they are diving. Measurements of $P_a$ were made under a static state, but diving is under a hydrodynamic regime. When a wing-propelled diving bird descends in the water column, both active downstroke and upstroke increases body acceleration. Plumage air pressure depends not only on depth, but also on speed and the gradient between the body's front and back during active strokes. If this pressure gradient is larger than the dynamical critical pressure resistance to air outflow, a loss of bubbles from plumage is expected.

## II.6.4 Wetting costs

Plumage wettability of aquatic birds results from the collective penetration resistance of all one-side wet feathers. When water penetration is high, it increases the birds' body mass significantly (Mahoney, 1984; Ortega-Jiménez et al., 2009). Aerodynamic theory predicts that induced power requirements, which are greatest at slow speed flight, increase with mass (Pennycuick, 1975). Ortega-Jiménez et al (2009) showed that wettability reduces

takeoff ability of alcids. The fact that one-side wet feathers resist water penetration helps to avoid excessive wetting costs.

Moreover, water penetration could reduce air content in plumage negatively affecting insulation and body heat maintenance. Anhinga, a wettable bird, increases their thermal conductance and heat loss 32% when wet (Mahoney, 1984). Mallard ducklings down coat saturated with water increases their thermal conductance ten-fold compared with that of dry down coat (Bakken, 2006).

**II.6.5 One-side wet feather benefits**

One-side wet feathers promote partial plumage wettability without water penetration. Despite aerodynamic costs due to plumage wettability for studied alcids, benefits could be enhanced attending that one-side wet feathers resist air outflow effectively. During each emersion after successive divings, feathers gradually increase their wetting. Thus, in agreement with our results, warm air outflow from plumage must be avoided. The positive effect of one-side wetting on air plumage retention must be beneficial to auklets and murrelets that forage in cool waters, despite aerodynamic costs.

# Chapter III

## Takeoff flight performance and plumage wettability in Cassin's Auklet, Xantus's Murrelet and Leach's Storm-petrel

## III.1 Abstract

Due to their marine habitats and distinctive foraging modes, seabirds face unique challenges with respect to flying that are negotiated differently by various species. One such challenge is taking-off from the water with wet plumage. This study evaluated plumage wettability and takeoff performance in three seabird species: two wing propelled divers with high wing loading, Cassin's Auklet *Ptychoramphus aleuticus* and Xantus's Murrelet *Synthliboramphus hypoleucus*; and Leach's Storm-petrel *Oceanodroma leucorhoa*, a surface feeder with low wing loading. The plumages of the diving birds held less water than that of the storm-petrel (~6.7% of body mass vs. 9.5%). This difference is explained by *O. leucorhoa's* surface to volume ratio larger than that of the alcids. Furthermore, the alcids have afterfeathers larger than those of the storm-petrel, which promotes a better insulation during diving. Examination of takeoff performance both before and after experimentally submerging the birds indicated that wingbeat frequency, speed and mass-specific power (peak and mean), and energy per wingbeat decreased in all species when plumage was experimentally wetted; whereas mean acceleration increased. *O. leucorhoa* was more strongly affected by wet plumage than the alcids, with a 32% of reduction in mass specific energy per wingbeat compared to ≤25% in the alcids. Takeoff angle was reduced in alcids, but not significantly so in *O. leucorhoa*. Results offer insights into the takeoff mechanics problems of wet seabirds given their differences in life history and morphology.

## III.2 Resumen

Los efectos mecánicos debidos al agua en el plumaje se evaluaron con relación a la habilidad de despegue de tres especies de aves marinas, dos álcidos y un hidrobátido: *P. aleuticus, S. hypoleucus,* y *O. leucorhoa*. Las dos primeras especies presentan un carga alar grande y utilizan las alas tanto para volar como para bucear; la tercera forrajea en la superficie del mar y presenta una carga alar baja. El agua retenida por el plumaje de los álcidos fue menor que la de *O. leucorhoa* (~6.7% de la masa del cuerpo vs. 9.5%). Esta diferencia se explica debido a que la razón entre la superficie y la masa del cuerpo es mayor en *O. leucorhoa* que en los álcidos. La evaluación del despegue de estas tres especies, antes y después de mojar experimentalmente su plumaje, resultó en una reducción de la frecuencia de aleteo, velocidad, potencia por unidad de masa (media y máxima), energía mecánica por aleteo. Pero la aceleración aumentó. Durante el despegue, *O. leucorhoa* redujo su energía por unidad de masa y por aleteo en un 32%, mientras los álcidos la redujeron ≤25%. El ángulo de despegue disminuyó en los álcidos, pero no en *O. leucorhoa*.

## III.3 Introduction

Anecdotal observations of seabirds suggest that wet plumage can reduce takeoff performance (Mahoney, 1984). Plumage wettability, which is defined as the percentage gain in body weight that a wet bird experiences, depends upon the properties of individual feathers (Rijke, 1968, 1970; Grémillet et al., 2005). Wet birds are heavier, with increased wing loading and energetic costs associated with flying (Mahoney, 1984). Feeding opportunities in a patchy habitat lead many seabirds to travel over large areas in search for prey. Hence, the cumulative effect of increased wing loading due to wet plumage can be considerable during a long foraging trip. However, birds generally shed water from their plumage as they fly, which would indicate that the negative effects of wet plumage are most important during takeoff.

Takeoff uses about four times the mass-specific mechanical power of cruising flight (Askew et al., 2001). Water absorbed by the plumage effectively increases wing loading, which decreases aerodynamic efficiency (i.e., lift:drag ratio), and increases the induced power requirements for flight (Pennycuick, 1975). Additionally, mass increment due to water retained by the wings could affect the moment of inertia during flapping, causing increased inertial power during the initial flap cycles of takeoff (Van den Berg and Rayner, 1995). Leg thrust, when employed in conjunction with wing flapping, reduces the demand on flight muscle power during takeoff, helping to maximize initial flight velocity (Earls, 2000; Tobalske et al., 2004). However, birds floating on the water cannot use leg thrust as effectively as birds on solid ground, which means that the wings must bear more of the burden for at-sea takeoffs (Norberg and Norberg, 1971). Hence, the negative effects of wet plumage on takeoff performance may be especially critical for seabirds. Nevertheless, there have been no detailed kinematic studies to quantify the effects of wet plumage on takeoff performance.

Seabirds capable of both flying and diving exhibit tradeoffs between selective forces associated with these two forms of locomotion. For example, larger mass increases flight costs, but decreases buoyancy costs, which facilitates diving (Lovvorn and Jones, 1994: Ribak et al., 2005). Most cormorants have a specialized feather structure that allows for a high degree of water penetration (Rijke, 1968; but see Grémillet et al., 2005). As a result, their plumage becomes soaked when they dive, which effectively reduces their buoyancy at the expense of reducing aerial takeoff performance.

Here, takeoff performance is examined as it relates to plumage wettability in three medium-sized seabirds: Cassin's Auklet *Ptychoramphus aleuticus*, Xantus's Murrelet *Synthliboramphus hypoleucus* and Leach's Storm-petrel *Oceanodroma leucorhoa*. Given that wet plumage causes an increase in mass, aerodynamic theory predicts decreases in takeoff angle, maximal acceleration, maximal speed and peak power for all species when the plumage is wet (Pennycuick, 1978; Hedenström, 1992). Similarly, a decrease of wingbeat frequency is predicted, given that water absorbed by the wing feathers will affect the rotational inertia of the wings (Van den Berg and Rayner, 1995).

*P. aleuticus* and *S. hypoleucus* are alcids, diving birds with relatively high wing loading and high flight costs (Roby and Ricklefs, 1986; Hodum, 1998: Table 1). *O. leucorhoa* is a sea-surface feeder with low wing loading and low flight costs, which rarely dives below the water surface (Manuwal, 1974; Murray et al., 1983; Huntington et al., 1996). Mahoney's (1984) comparison of plumage wettability in nine aquatic bird species suggested that surface feeders retain more water in their plumage than diving birds. Surface to volume ratio was calculated to explain differences in wettability of the three studied species.

## III.4 Methods

### III.4.1 Study species and sampling site

Study was conducted on West San Benito Island (28˚18' N, 115˚34' W), off the west coast of central Baja California. This island is close to the southern limit of each of the three species' breeding range. Data collection was carried out from 3 April through 28 May 2007. Mean air temperature at night was 11˚C (ranging from 7˚C to 13˚C); mean air pressure at sea level was 1008.8 hPa. The calculated air density was 1.234 kg m$^{-3}$.

### III. 4.2 Takeoff recording

Birds were caught with mist nets over the breeding colony or by hand using a spotlight when birds wandered around the ground at night. Birds were kept in cotton bags to reduce stress during transport to the experimental apparatus (transport usually took less than fifteen minutes). To ensure still air conditions, all takeoff trials were conducted in a hut (8 x 3.5 x 2.5 m). Birds were weighted ($m_b$) on an electronic balance (0.1 g accuracy).
Takeoff recordings began by placing a bird on a platform, 0.5 m above ground at one end of the hut. A mist net was positioned at the other end to prevent the bird from flying into a wall. Two video cameras recorded takeoffs simultaneously. Camera A (Sony HDR-UX1, 1440x1080i) recorded at 120 frames per second, and camera B (Sony DCRHC26,

720x480i) recorded at ~30 fps. Camera A was placed perpendicular to the designed flight path, and camera B was positioned behind the platform to record any lateral movement away from the designed path (Fig. 6). Birds were stimulated to takeoff with a loud vocal sound, which it was assumed would induce a maximal response during takeoff. Most birds responded immediately to the startle stimulus, but others needed more than one stimulus to initiate flight. Birds that did not fly after three minutes and birds that responded to the stimulus by running or jumping or colliding with the sides of the enclosure were not used in this study.

Each bird was weighed, induced to takeoff once, removed from the mist net, and allowed to rest for five minutes in a dark box. Birds were then submerged for five seconds in seawater, weighed a second time ($m_w$), and compelled to takeoff again. During submersion, birds were held loosely in one hand, allowing them to relax their wings, submerging the whole body for half a second and then leaving the head out for the bird to breathe for 4.5 s. Then, birds were kept in the hand in air for ten seconds to let excess water drip off. Mass of the water absorbed is $m_{wa} = m_w - m_b$. Plumage wettability was calculated as $[m_{wa}/m_b] \times 100$.
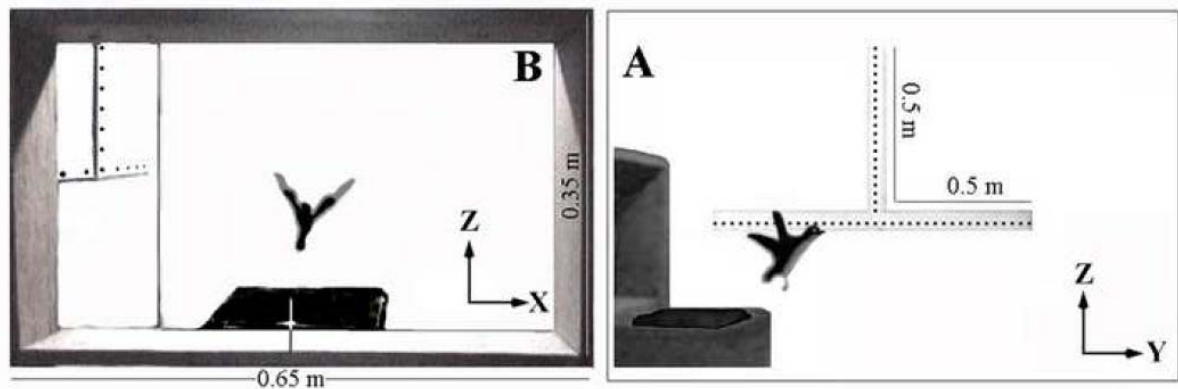


**Figure 6. Camera arrangement to film bird takeoffs with the X axis representing the horizontal axis of camera B, the Y axis representing the horizontal axis of camera A and both cameras share the vertical Z axis.**
**Figura 6. Arreglo de las dos cámaras usadas para filmar el despegue de las aves. El eje X representa el eje horizontal de la cámara B, el eje Y representa el eje horizontal de la cámara A y las dos cámaras comparten el eje vertical Z.**

**III.4.3 Video analysis**

To increase the effective frame rates used for analysis, footage from both cameras was de-interlaced using ProCoder 3 (Grass Valley), which doubled the frame rates to 240 and ~60 fps for cameras A and B, respectively. De-interlaced video sequences were transformed to JPG sequences. For each takeoff, the position of the upper part of the head was digitized as 3D coordinates, and that of the wingtip of the closest wing in 2D, beginning immediately after the bird's feet had left the platform.

Due to frame speed differences, the starting frame selected on the two camera sequences had a maximum synchronization error of 1/120 s, which was considered negligible. Frame-by-frame movement of each bird's head was digitized using Matlab, and the coordinates were transformed to meters using a calibration scale for each camera (Fig. 6). Bird position was determined using a 3D coordinate system, with the X axis representing the horizontal axis of camera B, the Y axis representing the horizontal axis of camera A and both cameras share the vertical Z axis (Fig. 1). A digitized data array of each camera-B sequence was interpolated using a cubic spline function to obtain the same number of digitized data points as the respective A data array. The apparent bird position was corrected for parallax to give actual position using the method of Askew et al. (2001), modified to be applied to the present reference system. Corrected x, y, and z coordinates were smoothed using a mean square error quintic spline with the FORTRAN program GCVSPL (Woltring, 1986) (Fig. 7). This quintic spline subroutine was used because it outperforms most other available smoothing methods and because it is the least biased and error prone (Walker, 1998). Digitization error variance of 1.58 $cm^2$ was obtained from ten repeated digitizations of the same takeoff sequence. The sequences of bird positions after corrections are shown in Figure 8. Smoothed coordinates from the splines were treated as functions of time, and first and second derivatives of these functions, with respect to time, were used to calculate the components of speed and acceleration. The vector magnitudes of total (3D) speed and acceleration were calculated and used to test takeoff performance.
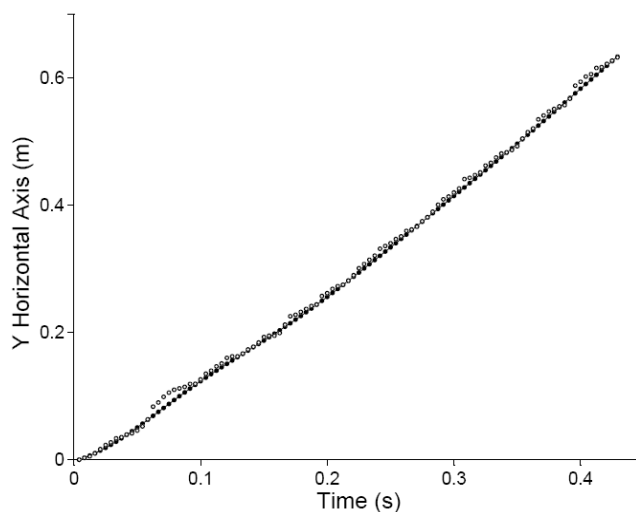
**Figure 7. Horizontal Y takeoff path of Cassin's Auklet. Frame-by-frame digitalization (open symbols) and mean square error quintic spline (close symbols).**
**Fugura 7. Trayectoria horizontal en Y del despegue de *P. aleuticus*. Digitalización cuadro por cuadro (símbolos abiertos) y spline quíntuple (símbolos cerrados).**
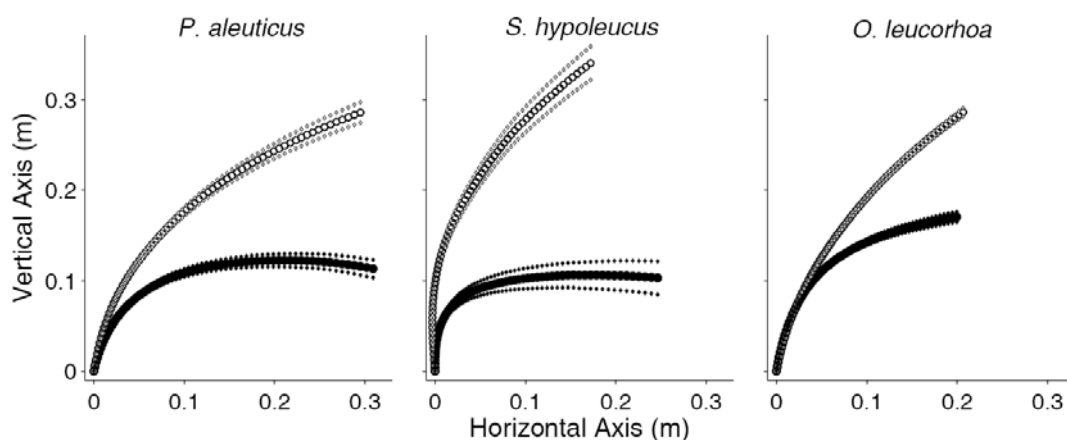


**Figure 8. Takeoff path of *P. aleuticus*, *S. hypoleucus*, and *O. leucorhoa*. Open and filled circles are means of dry and wet plumage conditions, respectively. Open and filled diamonds are the standard errors. Horizontal axis represents $(x^2 + y^2)^{0.5}$. Takeoff duration for all cases was 0.29 s (70 frames).**
**Figura 8. Trayectoria del despegue de *P. aleuticus*, *S. hypoleucus* y *O. leucorhoa*. Los círculos abiertos y cerrados representan respectivamente las condiciones de plumaje seco y mojado. Los rombos abiertos y cerrados representan el error estándar. El eje horizontal es $(x^2 + y^2)^{0.5}$. La duración de despegue en todos los casos fue 0.29 s (70 cuadros).**

To evaluate accuracy of the digitizing, parallax correction, smoothing and kinematic analysis, two ball-drop acceleration tests were conducted: falling ball and rolling ball in a 45° inclined plane (with respect to all three axis). The filming and correction procedure was

done as with the taking-off. For the fall test, the second derivative of the position of the ball as a function of time yielded a value for g of 9.78 m s$^{-2}$. For the rolling ball test, with a calculated friction coefficient of 0.08, it yielded 9.71 m s$^{-2}$. These figures are satisfactorily close to the 9.81 m s$^{-2}$ standard for acceleration due to gravity. Wingbeat frequency was obtained from the inverse of wingbeat period. Wingbeat period was calculated from wingtip position data, as the time between each successive wingbeat. Takeoff angle with respect to the horizontal ($\alpha = \tan^{-1}[\Delta z/(\Delta x^2+\Delta y^2)^{0.5}]$) was calculated at 0.04 seconds after takeoff. Mass-specific power $P_m$ was calculated as a dot product $P_m = (a + g) \cdot u$, where, $a = (a_x, a_y, a_z)$, $u = (u_x, u_y, u_z)$, and $g = (0, 0, -9.81)$ are the acceleration, speed and the gravitational acceleration vectors respectively. Mass-specific work per wingbeat was calculated by integrating $P_m$ through the four first wingbeat periods and dividing by four, following Swaddle et al. (1999). Similarly, mean speed and acceleration were calculated, both per wingbeat.

### III.4.4 Feather morphology

Twenty-five feathers from the breast were taken from one specimen of each of the three species to compare feather morphology. Afterfeather barbs of ten feathers were counted for each species. Feathers were flattened with a Petri dish to measure feather and afterfeather length. Then the length ratio ($r_f$) was calculated as: afterfeather length/feather length.

### III.4.5 Statistical analysis

One-way ANOVA was used to test for differences in plumage wettability and $r_f$ among the three species. For post-hoc comparisons Bonferroni's test was used with an alpha level of 0.05. Parallax correction, estimates of kinematic parameters and statistical analyses were performed in Matlab. Plumage wettability was square-root transformed to improve normality and equality of variances. Takeoff variables (peak speed, mean speed, peak acceleration, mean acceleration, mass-specific peak power, mass-specific energy, energy

and wingbeat frequency), except takeoff angle, were log transformed ($\log_{10}$) to satisfy ANOVA requirements for constant variance and normal distribution of error terms.

To test for the effects of wet plumage a repeated-measures ANOVA was performed on each of the takeoff performance parameters, with plumage condition (wet or dry) as the within-subject factor, 'species' as a between-subject factor. Data on 46 *P. aleuticus* individuals, 14 *S. hypoleucus* individuals, and 74 *O. leucorhoa* individuals were used in the repeated-measures ANOVA. Bonferroni post-hoc tests were used to identify significant differences. ANOVAs and post-hoc tests were carried out with SPSS v.12 (SPSS Inc., Chicago, IL, USA). In all statistical analyses, the probability level at which the null hypotheses of 'no difference' were rejected was $p > 0.05$. Henceforth, means are presented with 95% confidence intervals, wherein all calculations were carried out on the transformed scale and then transformed them back to the original scale.

## III.5 Results

### III.5.1 Plumage wettability

Water absorption did not differ significantly between the two alcids (one-way ANOVA, Bonferroni test, $p$ = 0.99), but the storm-petrel retained significantly more water than the alcids (Bonferroni test, $p<<0.001$). For *P. aleuticus* it was 6.8% (6.3%-7.2%), for *S. hypoleucus* it was 6.7% (6.0%-7.5%), and for *O. leucorhoa* it was 9.5% (8.8%-10.2%) of $m_b$ (Table 1).

*Table 1. Morphological data. Data shown are the mean (sample size, n within parentheses) with 95% CIs.*
*Tabla 1. Datos morfológicos. Se muestra la media (n) y el intervalo de confianza al 95%*

| Variable | *P. aleuticus* | *S. hypoleucus* | *O. leucorhoa* |
|---|---|---|---|
| Body mass 'dry' (g) | 149.8 (130) (147.7-151.9) | 156.9 (52) (153.5-160.3) | 42.4 (138) (41.9-43.0) |
| Body mass 'wet' (g) | 160.1 (130) (157.6-162.6) | 167.6 (52) (163.7-171.5) | 46.4 (138) (45.8-47.1) |
| Wing area (cm$^2$) | 208 (5) (197-219) | 213 (5) (20.3-22.4) | 253 (5) (247-259) |
| Aspect ratio | 7.9 (5) (7.2-8.7) | 8.1 (5) (7.5-8.7) | 7.9 (5) (7.3-8.4) |
| Wing loading (N m$^{-2}$) | 71.1 (5) (63.2-79.1) | 72.3 (5) (68.7-75.8) | 16.1 (5) (12.5-19.6) |

### III.5.2 Plumage morphology

In alcids the pennaceous feathers are more curved than in *O. leucorhoa* (not evident in Fig. 9 because feathers were flattened). In the ventral contour feathers of the storm-petrel, the central portion of the vane, close to the rachis, has a regular structure that contrasts with a loose, irregular proximal structure. For ventral contour feathers of the alcids, the entire vane has a loose irregular structure (Fig. 9). The length ratios $r_f$ were virtually the same for *P. aleuticus* and *S. hypoleucus*: 0.49 (0.48-0.51) and 0.51 (0.50-0.53) respectively (Bonferroni test, $p$ = 0.072). But, *O. leucorhoa* had a length ratio of 0.35 (0.34-0.36), which was significantly lower than those of the alcids (for both differences: Bonferroni test, $p<0.001$).

*P. aleuticus* had 28 (26-30) afterfeather barbs, *S. hypoleucus* 28 (25-30) and *O. leucorhoa* 26 (24-28).
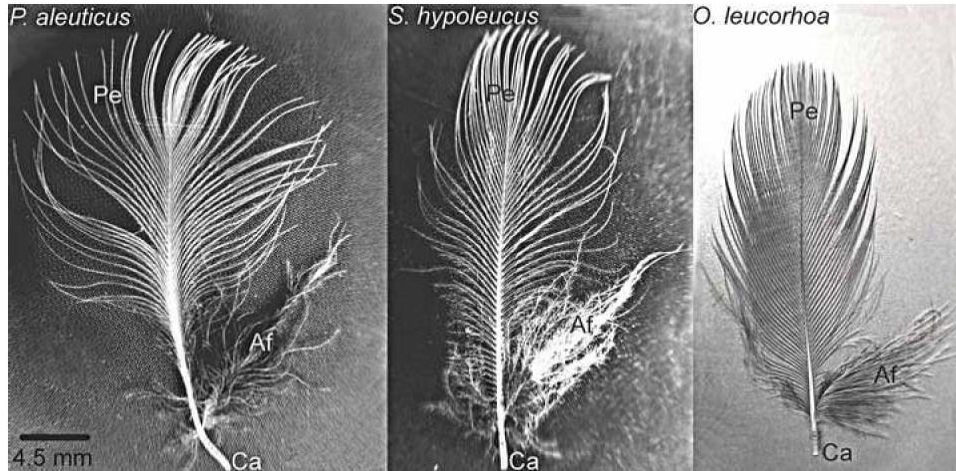


**Figure 9. Feathers of *P. aleuticus*, *S. hypoleucus*, and *O. leucorhoa*. Ca, calamus; Pe, pennaceous; and Af, afterfeather.**
**Figura 9. Plumas de *P. aleuticus*, *S. hypoleucus* y *O. leucorhoa*. Ca, calamus; Pe, penacho; y Af, hyporachis.**

### III.5.3 Takeoff performance and effects of wet plumage

Wet plumage decreased takeoff speed in all three species (peak speed: $F_{1,131} = 11.04$, $p = 0.001$; mean speed: $F_{1,131} = 35.44$, $p \ll 0.001$; Fig. 10a). *P. aleuticus* had the fastest takeoff of the three species as measured by peak and mean speed, regardless of whether plumage was wet or dry. Peak acceleration was not strongly affected by wet plumage ($F_{1,131} = 3.04$, $p = 0.083$) (Fig. 10b). Surprisingly, mean acceleration was higher for wet than for dry conditions ($F_{1,131} = 19.501$, $p < 0.001$). Mean acceleration for the alcids was greater compared to that of *O. leucorhoa* (Fig. 10b). Takeoff angle decreased when plumage was wet ($F_{1,131} = 28.76$, $p \ll 0.001$) but it was not significant for *O. leucorhoa* (Fig. 10c). Mass-specific peak power was lower in wet birds ($F_{1,131} = 5.63$, $p = 0.019$). Peak power appeared to be more strongly influenced by wet plumage in *S. hypoleucus*, than in the other two species (Fig. 10d). Similarly, mass-specific energy $E_m$ and energy $E$ (both per wingbeat) decreased with wet plumage in all three species ($E_m$: $F_{1,131} = 42.16$, $p \ll 0.001$; E: $F_{1,131} = 23.69$, $p \ll 0.001$) (Fig. 10e). Energy per wingbeat (not illustrated) for *P. aleuticus*

was 0.128 J (0.119 J - 0.137 J) and 0.109 J (0.095 J - 0.122 J) with dry and wet conditions respectively; for *S. hypoleucus* it was 0.125 J (0.111 J - 0.140 J) and 0.114 J (0.097 J - 0.131 J); and for *O. leucorhoa* it was 0.058 J (0.054 J - 0.061 J) and 0.044 J (0.041 J - 0.048J). Since $E_m$ was reduced in wet birds, the mean mass-specific power was also reduced (not illustrated). The effect of wet plumage on both $E_m$ and $E$ were strongest in *O. leucorhoa*. Wingbeat frequency decreased when plumage was wet in all three species ($F_{1,131}$= 128.6, *p*<<0.001). Wingbeat frequency was markedly lower in *O. leucorhoa* than in the alcids (Fig. 10f).
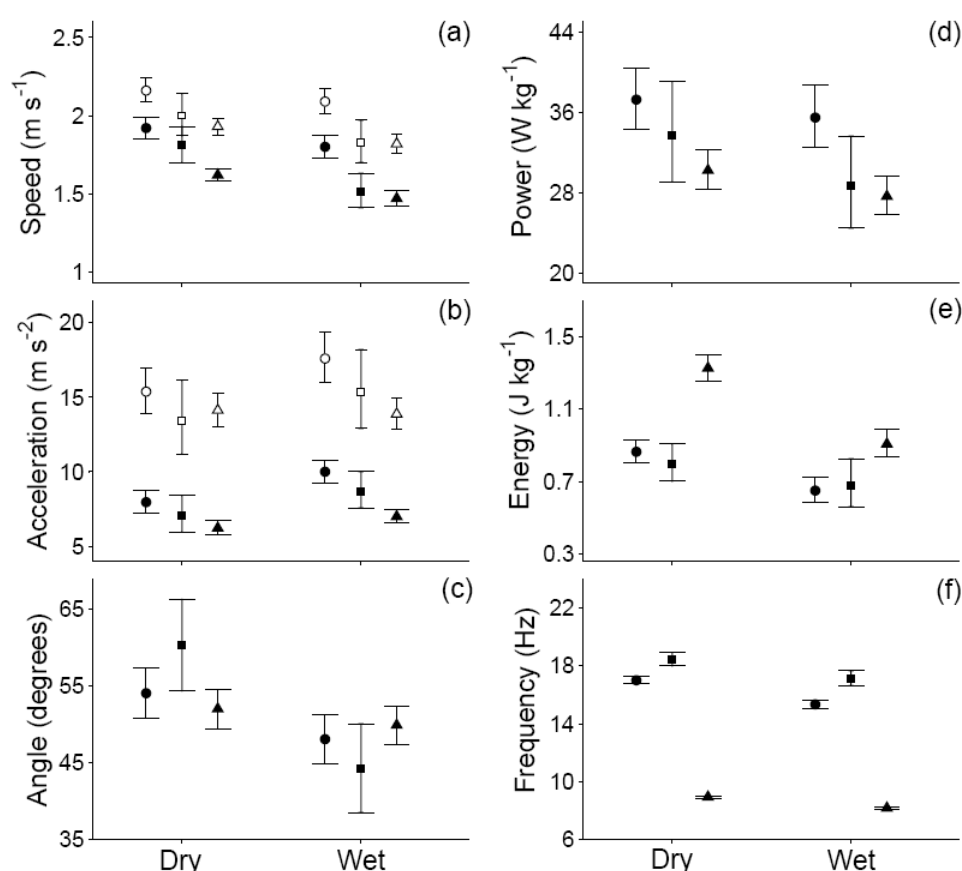


Figure 10. Comparison between dry and wet plumage conditions of the takeoff parameters for *P. aleuticus* (circles), *S. hypoleucus* (squares) and *O. leucorhoa* (triangles). (a) Peak speed (open symbols) and mean speed (filled symbols). (b) Peak acceleration (open symbols) and mean acceleration (filled symbols). (c) Takeoff angle. (d) Mass-specific mechanical peak power. (e) Mass-specific work per wingbeat. (f) Wingbeat frequency. Error bars indicate 95% confidence intervals.

Figura 10. Comparación entre las condiciones de plumaje seco y mojado de cada uno de los parámetros de despegue para *P. aleuticus* (círculos), *S. hypoleucus* (cuadrados) y *O. leucorhoa* (triángulos). (a) Velocidad máxima (símbolos abiertos) y velocidad media (símbolos cerrados). (b) Aceleración máxima (símbolos abiertos) y aceleración media (símbolos cerrados). (c) Ángulo de despegue. (d) Potencia máxima por unidad de masa. (e) Trabajo por unidad de masa y por aleteo. (f) Frecuencia de aleteo. Las barras representan los intervalos de confianza al 95%.

## III.6 Discussion

Mahoney (1984) found that wet birds gain an upper limit of 8% of body mass for surface feeders and 4% for diving feeders. These results are significantly higher than those of Mahoney (1984) (8.8%-10.2% and 6.0%-7.5%, for surface and diving feeders, respectively). These higher values could be due to differences in bird manipulation. Nevertheless, water retained by both diving birds (alcids) was significantly less than that retained by the surface feeder (storm-petrel), in agreement with Mahoney's (1984) results. Water retention differences could be explained attending the surface to volume ratios. Surface area may be estimated following Walsberg and King (1978) ($A_s = 8.11 \times 10^2 m_b^{0.667}$). If the volume of water absorbed is calculated as $V_w = m_{wa}/\rho$, where $\rho$ is 1027 kg m$^{-3}$, then a wet layer thickness ($V_w/A_s$) of ~0.4 mm was obtained for the three species. Hence, body size satisfactorily explains differences. Alcids and storm-petrels differ in their feather structure. The afterfeather role for water resistance is not clear. However, the afterfeather is mainly responsible for insulation in penguins (Dawson et al., 1999). Consequently the large size of afterfeathers in sampled alcids possibly serves to reduce heat loss during diving.

Leach's Storm-petrel is an opportunistic surface feeder, and it is known to forage at/or near the sea surface and rarely immerse into water (Huntington et al., 1996). Possibly, this feeding behavior allows for avoidance of plumage water absorbance and it is a strategy to reduce takeoff costs. In alcids wettability induce tradeoffs between flying and diving, with higher costs during takeoff and lower costs during diving.

Aerodynamic theory (Pennycuick, 1978) predicts that the induced power requirements, which are greatest at slow speed flight, increase with mass. However, the results in this study suggest that the mass increment of wet birds taking off do not satisfactorily explain the negative effect found in energy output per wingbeat. One possibility to explain this energy reduction is that the increased mass of the wings could have affected their rotational inertia. The inertial power required to accelerate and decelerate the wings during each wing stroke increases with the mass of the wings and the distance from the axis of rotation (Van den Berg and Rayner, 1995). Hence, water retained by the distal wing feathers could explain the observed decrease in flap rates associated with wet plumage.

Empirical studies of flight metabolic costs and artificially increased mass portray different scenarios. During long flights, Rock Doves, *Columba livia,* are negatively affected by loads as small as 5% of body mass (Gessaman and Nagy, 1988). In contrast, Zebra Finches, *Taeniopygia guttata,* and Cockatiels, *Nyphicus hollandicus,* making short flights with artificial payloads, appeared to adjust flight kinematics (speed and wingbeat frequency), while maintaining the same flight energy costs (Nudds and Bryant, 2002; Hambly et al., 2004). Strictly, none of these studies exclusively measured the metabolic cost of takeoff. The pigeons performed long trips, sustaining cruising-flights, whereas the short perch-to-perch flights of Zebra Finches and Cockatiels included numerous takeoffs, landings, ascents, descents, and maneuvers. However, Nudds and Bryant (2002) did include takeoff mechanical power calculations that agree with their metabolic findings with no extra cost due to payload. Direct comparison between present study and that of Nudds and Bryant (2002) is limited by some important methodological differences. First, takeoffs measured by Nudds and Bryant (2002) were not associated with escape behavior. Also, the mass-specific energy per wingbeat was used to evaluate takeoff performance, which integrates the effect of ascent angle, speed, and acceleration (as in Swaddle et al., 1999). Conversely, Nudds and Bryant (2002) were concerned with the mechanical energy gained between the eighth and ninth video frames (0.04 s) after takeoff. In addition, Nudds and Bryant (2002) used artificial loads placed on each bird's back in such a manner as to avoid changes to the center of mass, drag, and wing mobility. Due to flapping removing absorbed water, and also to differences in the structure of flight feathers and the rest of the plumage, the wet-plumage treatment possibly resulted in a non-uniform distribution of added mass. These may have affected the wing stroke as well as flight power requirements.

The negative effect of wet plumage on most of the kinetic variables was expected. Most surprising was the fact that *P. aleuticus* had much higher peak and mean speed than the other alcid. This finding may be related to leg thrust (Earls, 2000). Auklets have larger legs and shorter pelvic bones than Xantus's Murrelets (Storer, 1945). Unfortunately, leg thrust was not measured. Another notable difference between the two alcids was that wingbeat frequency was higher for *S. hypoleucus* than for *P. aleuticus*. Because the morphologies of the two alcids are very similar, a simple explanation for this discrepancy is not evident, but

consideration of their life histories, especially behavioral differences in rearing chicks, may explain why *P. aleuticus* demonstrated greater takeoff speed with a lower flap rate. The chicks of *P. aleuticus* rely on provisioning at the nest for three to four weeks (Manuwal, 1974; Murray et al., 1983). Therefore, breeding *P. aleuticus* must deliver food to their nestlings for an extended period of time, and presumably the provisioners would benefit from delivering maximal food loads as opposed to making a large number of trips. Conversely, *S. hypoleucus* chicks fledge two days after hatching and are not provisioned until their join their parents on the water (Murray et al. 1983). Hence, the need for provisioning young at the nest may increase selective pressures associated with flight and load-bearing in *P. aleuticus* relative to *S. hypoleucus* and these pressures may account for the superior takeoff performance in the former.

One unexpected result was that wet plumage did not affect takeoff angle (at $t = 0.04$ s) in *O. leucorhoa*. This finding may be related to the relatively low wing loading of this species and the proportionally high potential to generate lift (Pennycuick, 1978). Moreover, storm-petrels have large tails that may aid in lift production (Thomas, 1993). Finally, the increase in mean acceleration associated with wet plumage may seem puzzling at first, but it is likely due to the continuous loss of water during takeoff. Instantaneous acceleration experienced by the body of a flying bird during a wingbeat is the ratio of the instantaneous force acting on it and its mass. Thus, if mass is reduced with time an increase of acceleration is expected. Unfortunately, the rate of water loss was not measured, but there is little doubt that water loss occurred throughout each experimental flight. An alternative explanation (for alcids) could be that mean acceleration increased due to the decrease of takeoff angle, because it permits a higher total acceleration due to a larger horizontal component. Possibly, both water loss and the decrease of takeoff angle caused mean acceleration to increase.

There are a number of factors that can influence takeoff performance, including leg-thrust, wind, wing morphology, and any mass increment. Leg thrust can contribute significantly to takeoff acceleration (Earls, 2000; Tobalske et al., 2004). Although in the experiments birds were taking off from a solid substrate that permitted leg thrust, for birds at sea a solid

substrate is lacking and leg thrust is either not used or of little use. On the other hand, if birds can run over the sea surface it is expected that energy cost of takeoff decreases.

Wind can greatly facilitate takeoff (Pennycuick, 1978), and storm-petrels may be better able to exploit headwinds when taking off due to their low wing loading and relatively long wingspan. Even the slightest breeze may allow them to offset the flight costs associated with food intake and wet plumage (Withers, 1979). Alcids, however, are wing-propelled divers, with higher wing loading and shorter wingspans than storm-petrels. Aerodynamic theory predicts a low aerodynamic efficiency for these species (Pennycuick, 1975). For that reason, wind speed has to be relatively high to have an important effect on takeoff performance. Given these constraints as well as the fact that alcids are far more likely to dive underwater, one would expect alcids to have more waterproof plumage to reduce their water load and decrease energy costs associated with takeoff but, as it was mentioned above, absorbed water thickness was the same in all three studied species.

An obvious strategy for avoiding the effects of wet plumage on takeoff is to dry the plumage to some extent. Birds at sea often expel water from their feathers by shaking their wings, head, tail, or in some cases their whole body. Seabirds may also adopt postures that facilitate evaporation by sun and wind exposure. For example, most cormorants spread their wings to the sun and/or breeze after a period in the water, suggesting that they are drying their plumage (Rijke, 1968; Sellers, 1995). For diving birds, like alcids, these simple behavioral responses could reduce takeoff costs considerably.

Food intake and plumage wettability increase body mass of seabirds. During the reproductive season, storm-petrels could carry food representing 23% of their body mass (Pitman and Ballance, 1990). Meanwhile auklets carry back to the island a food mass which represents 11% of their body mass (Speich and Manuwal, 1974). Adding water mass due to plumage wettability to food mass, according to the results in this study, imply that alcids can increase body mass up to ~18% and the storm-petrel can do it up to ~33 %. Nevertheless, it is difficult to say if wettability has a smaller effect than food loading on takeoff of these three species. Results from this work suggest that wettability could affect rotational inertia of the wings.

# Chapter IV

## Short-burst maximum lift and power production of three medium-size seabirds

## IV.1 Abstract

Seabirds face unique aerodynamic problems relative to their life histories. At sea, birds increase wing loading as a consequence of plumage wettability and food consumption reducing their flight performance. It is expected that maximal load supported by a seabird occurs during takeoff. In flying birds, load carrying capacity and potential power production are important determinants of how birds interact with their environment, yet there are few comparative studies to permit insights into how these parameters may relate to behavioral adaptations and life histories, especially in aquatic species. Empirical evaluation of maximum load-lift and induced power production during takeoff was performed for three seabird species, a storm-petrel and two alcids: Leach's Storm-petrel *Oceanodroma leucorhoa*, Cassin's Auklet *Ptychoramphus aleuticus,* and Xantus's Murrelet *Synthliboramphus hypoleucus*. Leach's storm petrel supported a mean maximum extra load of 45% of its body mass, Cassin's Auklet supported 23%, and Xantus's Murrelet 21%. Mean maximum induced power output was 0.7 W for Leach's Storm-petrel, 4.5 W for Cassin's Auklet, and 5.7 W for Xantus's Murrelet. Based on data from the literature, results on maximum load and its relation with food transport and plumage wettability were discussed.

## IV.2 Resumen

Las aves marinas incrementan su masa principalmente por el alimento que ingieren, las reservas de grasa que almacenan en el cuerpo y por el agua absorbida por el plumaje. Estos tres factores son máximos durante la época reproductiva, debido a las demandas energéticas altas que impone la crianza de los pollos. Tales factores incrementan los costos de vuelo y en especial los de despegue. En el presente estudio se reportan los resultados de los experimentos de máxima carga durante el despegue de tres especies de aves marinas, dos álcidos y un hidrobátido: *P. aleuticus, S. hypoleucus,* y *O. leucorhoa*. Las dos primeras presentan un carga alar grande y utilizan las alas tanto para volar como para bucear; la tercera forrajea en la superficie del mar y presenta una carga alar baja. *O. leucorhoa* soportó una carga extra del 45% con relación a su masa; mientras que *P. aleuticus* soportó 23% y *S. hypoleucus* 21%. La potencia máxima inducida para *O. leucorhoa* fue 0.7 W, para *P. aleuticus* 4.5 W y para *S. hypoleucus* 5.7 W. Basado en datos de masa de la literatura, se discuten los resultados de máxima carga y su relación con el transporte de alimento y absorción de agua en el plumaje.

## IV.3 Introduction

Seabirds face unique aerodynamic challenges in relation to their life histories that are negotiated differently by various species. One such challenge is takeoff from water with increased body mass. Aerodynamic theory predicts that positive changes in body mass significantly affect flight power requirements (Pennycuick, 1978). Body mass of seabirds increases as a consequence of eating large food items (usually fish) and by high body fat stores before migration and reproduction. Plumage wettability also contributes to increased mass of seabirds by about ten percent (Mahoney, 1984; Ortega-Jiménez et al., 2009). Thus, it is expected that birds taking-off from sea face near-maximal wing loading for flight given the combined effects of food consumption, fat storage, and plumage wettability. Common

Eider's females experience a 'temporary flightlessness' during reproductive season due to a 20% body mass increase (Parker and Holm, 1990; Guillemette and Ouellet, 2005).

Flying animals require relatively high capacity for power and lift production to become airborne (Askew et al., 2001). The maximum load supported during short-bursts of flying animals seems to be positively correlated with muscle mass (Marden, 1987; 1990). Using ten terrestrial bird species, Marden (1990) concluded that maximum induced power output (which is the cost of lift production) can be predicted using the actuator-disk equation for hovering flight (Weis-Fogh, 1972), and some morphologic measurements (i.e. body mass, maximum load and wing semi-span).

In this study, the maximal load-lift production and induced power output was evaluated for three medium-sized seabirds: Leach's Storm-petrel *Oceanodroma leucorhoa,* Cassin's Auklet *Ptychoramphus aleuticus*, and Xantus's Murrelet *Synthliboramphus hypoleucus.* Cassin's Auklet and Xantus's Murrelet are wing-propelled divers of the family Alcidae (Manuwal, 1974; Murray et al., 1983; Huntington et al., 1996), and they maintain higher wing loading than surface-feeding storm petrels (Hydrobatidae). Results of this study were compared with data reported in the literature on food intake and plumage wettability. Also, results were compared with the values predicted by Marden (1990).

## IV.4 Methods

### IV.4.1 Study species and sampling site

The study site was located at West San Benito Island (28˚18' N, 115˚34' W), off the west coast of central Baja California. All study species forage at sea during the day and return to their breeding colony only at night. Leach's Storm-petrel and Cassin's Auklet are widespread throughout the North Pacific, whereas Xantus's Murrelet breeds no farther north than Point Conception, California. San Benito Island is close to the southern limit of each of the three species' breeding range. Cassin's Auklet and Xantus's Murrelet are wing-propelled divers, and their wing morphology represents a compromise between the requirements of flight and diving. Consequently, the energetic costs of flight are high for

alcids (Roby and Ricklefs, 1986; Hodum, 1998). Leach's Storm-petrel is an opportunistic surface feeder, and it is known to forage on a variety of plankton and nekton at or near the sea surface (Huntington et al., 1996). Its wing loading is considerably less than that of the two alcids (Table 2).

Data collection was carried out from 15 through 28 May 2007. Mean air temperature was 11˚C; mean air pressure at sea level was 1008.8 hPa. Air density from these values is 1.234 kg m$^{-3}$ (Pennycuick 1989). All methods were approved by the Mexican Secretaría de Medio Ambiente y Recursos Naturales to grant the permit for the study (Oficio Num/SGPA/DGVS/01081).

## IV.4.2 Maximum load-lift

Twenty six Leach's Storm-petrels, nineteen Cassin's Auklets, and one Xantus's Murrelet were used to evaluate the mean maximum load capacity for each species, following Marden (1987). Five plastic pellets (0.3 g each) were progressively added to a plastic bag (0.9 g) fixed to the legs. Care was taken so that bag attachments did not impede leg movements. Birds were placed on a platform and stimulated to fly. More weight was added after each takeoff until they could no longer takeoff (i.e., the bird was unable to move forward and upward). Two minutes of rest inside a cage were permitted between each flight. Maximal load was calculated as the mass halfway between the maximum mass lifted (body mass plus added loaded mass) and the minimum mass with which the animal could not lift. Maximal lift force (N) was calculated as the product of maximal load and gravity acceleration $g$. Maximum induced power output was estimated using maximal lift values in agreement with the actuator-disk theory, following Marden (1990).

**IV.4.3 Muscle mass measurements**

One specimen of each species was measured for total muscle mass ($M_{tmus}$). Each of these specimens had been injured by cactus spines (Cassin's Auklet and Leach's Storm-petrel) or by a crash against a fisherman's house (Xantus's Murrelet). Birds were sacrificed and dissected. The entire pectoral, ventral, dorsal and wing musculature was dissected and weighed. Marginal muscle ratio ($M_{tmus}/(m_b + M_L)$) was calculated for each species (Marden, 1987). Total muscle mass is $M_{tmus}$, $m_b$ is the body mass, and $M_L$ is the loaded mass.

**IV. 4.4 Statistical analyses**

To test for maximal load significant differences between the surface feeder and the diving birds, a Student's t-test was applied to data for 26 storm-petrels and 19 Cassin's Auklets. The single maximal load measurement of Xantus's Murrelet did not provide for degrees of freedom. In all statistical analyses, the probability level at which the null hypotheses of 'no difference' was rejected is $p = 0.05$. In what follows, when a mean is presented followed by a value within parentheses (i.e., ± a value) it is the standard error.

# IV.5 Results

Maximum lift per unit of flight muscle mass differed significantly between Cassin's Auklet and Leach's Storm-petrel ($t_{43} = -11.29$, $p << 0.001$). The mean for Leach's Storm-petrel was 83.7 (±1.27) N kg$^{-1}$, for Cassin's Auklet it was 62.1 (±1.18) N kg$^{-1}$, and for Xantus's Murrelet it was 63.4 N kg$^{-1}$. Marginal muscle ratio was 0.12 for Leach's Storm-petrel, 0.157 for Cassin's Auklet, and 0.156 for Xantus's Murrelet (Table 2). The mean maximal extra load supported (added mass) was 18(±1.18) g for Leach's storm petrel, 35.89(±0.6) g for Cassin's Auklet, and 39.65 g for Xantus's Murrelet. These values correspond to 45% (±0.5), 23% (±2.1), and 21% of the body mass, respectively. The mean maximum induced power output for Leach's Storm-petrel was 0.7(±0.016) W, Cassin's Auklet was 4.5(±0.11) W, and 5.7 W for Xantus's Murrelet (Table 2).

**Table 2 Morphology and muscle mass measurements. Data shown are the mean ± SE (n).**
**Tabla 2. Medidas de morfología y masa muscular. Se muestra la media ± error estándar (n)**

| Variable | *P. aleuticus* | *S. hypoleucus* | *O. leucorhoa* |
|---|---|---|---|
| Body mass 'dry' (g) | 152.5 ± 2.21(19) | 185.2 (1) | 40.1± 0.64(26) |
| Max. load (g) | 188.48±3.83(19) | 224.85(1) | 58.1±1.23(26) |
| Max. lift (N) | 1.86±0.04(19) | 2.2(1) | 0.57±0.01(26) |
| Max. $P_i$ (W) | 4.5(±0.11) | 5.7 | 0.7(±0.016) |
| Pectoralis mass(g) | 21.5(1) | 28.4(1) | 4(1) |
| Muscle mass[1](g) | 30(1) | 35(1) | 6.8(1) |

[1] The entire pectoral musculature, ventral, dorsal and along the wing bones.
[1] La musculatura total del pectoral, ventral, dorsal y a lo largo de los huesos del ala.

## IV.6 Discussion

Results on maximal load-lift, maximum induced power and marginal flight muscle ratio of Cassin's Auklet and Xantus's Murrelet, roughly agree with Marden's (1987; 1990) results. This agreement is not surprising because alcid's pectoralis muscle, the most important muscle for power flight, has a similar proportion to body mass as in non-diving species (Kovacs and Meyers, 2000). In contrast, Leach's Storm-petrels showed a greater maximal load than the one predicted as a function of flight muscle by Marden's (1987) regression model. On the other hand, maximum induced power output of the storm-petrel was lower than the value predicted as a function of body mass by the regression model for terrestrial birds. These differences could be explained taking into account the storm-petrel morphology. Small wing loading allows a high aerodynamic efficiency, reducing induced power costs (Pennycuick 1978). Also, large tails can produce lift in a very similar way to conventional delta-wing models, within acceptable limits of tail spreads and angles of attack (Thomas, 1993; Evans, 2003). Therefore, in this species a high muscle mass is not necessary to produce sufficient lift.

**IV.6.1 Ecological implications**

Food intake could increase body mass considerably in seabirds. In fact, during reproductive season, egg production, incubation and chick rearing, seabirds increase their energy requirements and are forced to consume more food. Cassin's Auklets perform one trip per day to feed their chicks (from the island to the ocean and back), and it has been reported that they carry back to the island a mean food mass of 20 g, which represents 11% of their body mass (Speich and Manuwal, 1974). If water mass absorbed by the plumage is considered the total amount of mass increment (food plus water-load) would be 30 g. Maximal load results indicate that during takeoff Cassin's Auklets could be loaded with an extra mass of up to 38 g. Thus, these birds are left with a reduced safety load margin of ~4.5% of their body mass. Hodum et al. (1998) estimated that adults of this species might need to consume 67% of their body mass (mainly euphausiids) throughout the whole day during chick rearing to satisfy their energy demands. On the other hand, for Leach's Storm-petrel the mean stomach content is 8.5 g, which represents 23% of their body mass (Pitman and Ballance, 1990). Considering the water mass absorbed by its plumage, the amount of loaded-mass would be 12.5 g. Maximal load results indicated that during takeoff Leach's Storm-petrels could be loaded with an extra mass up to 16.5 g. Thus, for this species the safety load margin is ~11% of its body mass. An estimate of this species' food requirement suggests a consumption of 23 g throughout the whole day, or 50% of its body mass (Montevecchi et al., 1992).

Xantus's Murrelet consumes mostly euphausiids and northern anchovies (Hamilton et al., 2004), but little is known about daily food and energy requirements. Egg production and incubation by Xantus's Murrelet requires a high food supply, but the early departure of chicks from the nests allows adults to feed them directly at sea (Murray et al., 1983). Considering the alcids, Xantus's Murrelet's eggs are large relative to adult body mass. The mean weight of their eggs is 37 g. Xantus's Murrelet specimen used here had a body mass of 185 g, with an extra mass support of 39 g, which is very close to the egg's weight, leaving a very small safety margin for takeoff. Thus, less water absorption by the female plumage could facilitate takeoff. When incubating, weight changes of adults amounts to 10g

(Murray et al., 1983). Again if water mass absorbed by the plumage is considered, in the extreme case, the mass-loaded would be 17 g (weight increase plus water-load). This represents a safety load of ~6.5% of the body mass a similar percent value as that of Cassin's Auklet and lower than that of Leach's Storm-petrel. However, this value is for the incubation period only. These load estimations suggest that diving birds with non-precocious chicks, like Cassin's Auklets try to maximize the amount of food load for their chicks, in spite of larger takeoff and cruising flight costs. Meanwhile, Xantus's Murrelets apparently do not try to maximize the amount of food load during incubation, and possibly during chick rearing, because chicks are fed at sea. Also, incubation shifts by both parents are sporadic and changes in body mass do not represent a serious problem for takeoff. Moreover, eggs are frequently unattended (Murray et al., 1983).

# Chapter V

# Effects of air content changes on diving performance of two small alcids

## V.1 Abstract

The partial loss of air from plumage and/or respiratory system of aquatic birds can not only reduce buoyancy costs, but also improve diving performance. Hydrodynamic theory predicts that buoyancy variations produced by air volume changes can affect the speed of descent. Diving performance was tested experimentally increasing the air volume (16% of the original content with a low density polyethylene vest) of Cassin's Auklet and Xantus's Murrelet, compared with two control groups (one non-manipulated and one with a neutral buoyancy vest). Also, the loss of air (as bubbles) with time was measured. Manipulated birds, loaded with an artificial air vest, reduced their descent speed, distance per flap, and work per flap compared with non-manipulated birds of both alcids. Significant differences were found in the flap duration of auklets only. In contrast, no differences were found in the loss of air volume and the cost of transport between experimental groups of both alcids. Non-manipulated birds presented a higher drag than buoyancy; whereas buoyancy exceeded drag in manipulated birds. The air volume loss by Cassin's Auklet and Xantus's Murrelet measured during divings down to 0.7 m depth was 9% and 8% of the total air volume, respectively. At ~1.5 s of diving, the maximal loss of air estimated for both alcids from a regression model indicates a 12% loss with respect to initial air volume. These bird species use foot paddling as a complement of their wing propulsion. Results suggest that the reduction of the air volume could improve the descent speed of diving in small size

alcids. Heat costs and food intake benefits are discussed in relation with the loss of air and descent speed of both alcids.

## V.2 Resumen

En aves acuáticas la pérdida de aire del plumaje y/o el sistema respiratorio, no sólo reduce los costos por flotabilidad sino también facilita la habilidad de buceo. La teoría hidrodinámica predice que la velocidad de descenso de las aves marinas puede ser afectada por variaciones de flotabilidad producidas por cambios en el volumen de aire. La habilidad de buceo fue evaluada incrementando experimentalmente el volumen de aire en *Ptychoramphus aleuticus* y *Synthliboramphus hypoleucus* (16% más del contenido original con un chaleco de polietileno de baja densidad)*,* y comparando ésta con dos grupos de control (sin carga y con un chaleco con flotabilidad neutra). Además, se cuantificó la pérdida de aire (burbujas) con respecto al tiempo. En ambas especies, los especimenes manipulados redujeron su velocidad de descenso, distancia por aleteo y trabajo por aleteo en comparación con los controles, pero no hubo diferencias significativas entre controles. Sólo *P. aleuticus* mostró diferencias significativas en el periodo de aleteo. Sin embargo, en ninguna de las dos hubo diferencias significativas en la pérdida de volumen de aire y en el costo de transporte, entre grupos experimentales. Los controles mostraron un arrastre más alto que la flotabilidad; mientras que en las aves manipuladas fue al revés. El volumen de aire perdido por *P. aleuticus* y *S. hypoleucus* en buceos de hasta 0.7 m de profundidad fue respectivamente 9% y 8% del contenido total de aire. Se estimó que a los ~1.5 s de iniciado el buceo, la máxima pérdida de aire fue 12 % con relación al volumen de aire inicial, en ambos álcidos. Ambos álcidos usan las patas para propulsarse como complemento a la propulsión de las alas. Los resultados sugieren que la reducción de aire en el plumaje aumenta la velocidad de descenso de álcidos pequeños. Se discuten los costos por pérdida de calor corporal y los beneficios en la captura de presas, con relación a las perdidas de aire y la velocidad de descenso de ambos álcidos.

## V.3 Introduction

Diving birds must overcome three hydrodynamic components to move underwater: acceleration reaction, drag and buoyancy. Added mass appears from unsteady motion when an object accelerates in a fluid to increase the kinetic energy of both object (body inertia) and fluid (added mass). Acceleration reaction depends on size, shape and body acceleration (Daniel, 1984). In foot-propelled divers, inertial work accounts for 49-54% of total work (Lovvorn et al., 1991; but see Stephenson, 1994) during the stroke descent power phase. Nevertheless, this component could be neglected if average speed is relatively constant from one stroke cycle to the next, because the negative inertial work during passive phases of the stroke cycle counteracts positive inertial work during active stroke phases. On the other hand, empirical measurements of the hydrodynamic drag of frozen birds (in a water tank) indicate a power growth relationship with speed (Lovvorn et al., 2001). Diving at low speed reduces drag costs, but could negatively affect the maximal depth achieved by a bird. Buoyancy is not only reduced with increasing depth, as a consequence of Boyle's law but also by losses of air from plumage and/or respiratory system (Wilson et al., 1992). For Lesser Scaup *Aythya affinis,* compression due to hydrostatic pressure and the loss of air from plumage decreases buoyancy by 32% (Stephenson, 1994). Moreover, it has been suggested that in cormorants plumage wettability (up to 6% of body mass) could reduce the air content in plumage, reducing buoyancy by 18% (Ribak et al., 2005). On the other hand, air from the respiratory system could be reduced in a bird making dives following exhalation, as has been observed in great cormorants and some ducks (Ross, 1976; Tome and Wrubleski, 1988). Also, shallow diving penguins exhibit a reduced air volume in their respiratory system to avoid high buoyancy costs (Sato et al., 2002; 2006).

Theoretically, speed appears to be affected by buoyancy changes due to hydrostatic pressure. Lovvorn et al. (1999) developed a biomechanical model assuming that the stroke frequency and the work per flap stay constant as buoyancy changes with depth. This model predicts a gradual increase in speed with depth up to an asymptotic maximal speed. However, empirical data show that medium size alcids maintain a relatively constant swimming speed during descent (Lovvorn et al., 1999; Watanuki et al., 2006). Nonetheless,

Lovvorn's et al. (1999) model failed to predict measured speed, which may be because it does not take into account air losses from plumage and respiratory system during the first meters of depth. It is possible to reach close to maximal speed rapidly (few seconds) when taking into consideration these air losses.

Alcids are wing-propelled birds with relatively high wing loading, capable of both flying and diving, and with tradeoffs between selective forces associated with these two forms of locomotion. Similar to penguins (Clark and Bemis, 1979; Hui, 1988), alcids use an active, thrust-producing, upstroke as well as an active downstroke in forward propulsion underwater (Johansson and Aldrin, 2002). Swimming speed, drag, upstroke thrust and efficiency have been investigated in medium size alcids, and also the effect of molt on these variables (Lovvorn et al., 1999, 2001; Johansson and Aldrin, 2002; Bridge, 2004; Watanuki et al., 2006). However, diving of small alcids, like that of murrelets and some auklets has been described usually only in theoretical studies (Lovvorn and Liggins, 2002). This is due to limitations imposed by the size of measuring devices attached to the birds.

Auklets and murrelets feed on euphausiids and epipelagic schooling fishes (Hodum et al., 1998; Hamilton et al., 2004), and for them to capture prey they possibly exhibit both underwater undulations and V-shaped dives (Kuroki et al., 2003; Hamilton et al., 2005). Allometry of these species predicts a maximum diving duration of up ~50 s (an average of ~30 s) (Watanuki and Burger, 1999).

The main objective of this study is to quantify the effects of buoyancy increases – due to artificial air content increments, on diving performance of two small alcids (Cassin's Auklet *Ptychoramphus aleuticus,* and Xantus's Murrelet *Synthliboramphus hypoleucus*) and discuss these data in relation with results from the biomechanical model of Lovvorn et al. (1999). The null hypothesis, that buoyancy increase does not affect diving speed, was tested.

# V.4 Methods

### V.4.1 Study species and sampling site

The study site was located at West San Benito Island (28˚18' N, 115˚34' W), off the west coast of central Baja California. The two study-species forage at sea during the day and return to their breeding colony only at night. *P. aleuticus* are widespread throughout the North Pacific, whereas *S. hypoleucus* breeds no farther north than Point Conception, California. San Benito Island is close to the southern limit of each of the two species' breeding range. Data collection was carried out in May 2007. All methods were approved by the Mexican Secretaría de Medio Ambiente y Recursos Naturales to grant the permit for the study (Oficio Num/SGPA/DGVS/01081).

### V.4.2 Diving recording

Most *P. aleuticus* were caught with mist nets over the breeding colony. All *S. hypoleucus* and the remaining *P. aleuticus* were captured by hand using a spotlight when birds wandered around the ground at night. Birds were kept in cotton bags to reduce stress during transport to the experimental tank (transport usually took less than fifteen minutes). Birds were weighted ($m_b$) on an electronic Ohaus Scout balance (0.1 g accuracy). We conducted all diving trials in a tank (1.25 x 1.25 x 1 m) filled with water up to 0.7 m depth. Diving recording was done through a Plexiglas window (35 x 70 cm) at one side of the tank. Each bird was placed into the tank before any experimental trial so that it could adapt itself to the artificial diving conditions. Eight minutes later it was recaptured carefully by hand.

Diving recordings began by placing a bird on the water by hand. A camcorder (Sony HDR-UX1, 1440x1080i, 120 fps) was placed two meters from the Plexiglas window. Each diving trial was as follows: a person held a bird on the water surface for few seconds so that it would calm down. Then, the bird was released (without pushing it) while it was stimulated with a loud vocal sound, which we assumed would induce a maximal muscle-power response during diving. Most birds responded immediately to stimulus. Birds that did not

dive immediately after release or that crashed into the Plexiglas window were not used in this study. Only recordings of vertical dives were used.

## V.4.3 Experimental groups

Each bird was induced to dive three times: once without any sort of attachment (control group); once with a polyethylene vest filled with air (manipulated group); and a final dive with a glue-stick vest with near-neutral buoyancy (manipulated-control group). Density of vests was measured using the water displacement method. Density was 240.5 kg m$^{-3}$ and 971 kg m$^{-3}$ for polyethylene and glue-stick vests, respectively. Mass of both vests was 3.7 g. Polyethylene vest had a total volume of 1.54 x10$^{-5}$ m$^3$ (15.4 ml) and an air volume of 1.14 x10$^{-5}$ m$^3$ (11.4 ml). Volume of vests was based on the results reported by Stephenson (1994) on air lost during diving of Lesser Scaup. After its third trial, each bird was dried with a cotton towel and released in the same location where it was captured. Mean body mass of sampled Cassin's Auklets ($m_b$) was 0.153 (±0.0024) kg and that of Xantus's Murrelets was 0.155 (±0.0020) kg, where numbers within parentheses are SE (s n$^{-0.5}$).

## V.4.4 Depth, speed and acceleration

To increase the effective frame rates used for analysis, footage from camcorder was de-interlaced using ProCoder 3 (Grass Valley), which doubled the frame rate to 240. De-interlaced video sequences were transformed to maximum-quality JPG sequences. For each dive, the position of the beak tip was digitized as coordinates in two dimensions frame-by-frame using Matlab v. 7 and the coordinates were transformed to meters, taking water level as the vertical coordinate origin. Only the vertical component was used in the analysis. Vertical coordinates were smoothed using a mean square error quintic spline with the FORTRAN program GCVSPL (Woltring 1986). Digitization error variance of 1.5 cm$^2$ was obtained from ten repeated digitizations of the same diving sequence. Smoothed vertical coordinate ($y$) from the spline were treated as function of time, and first and second derivatives of that function, with respect to time, were used to calculate vertical descent

speed ($u_y$) and acceleration ($a_y$). Flap cycle duration (s) was calculated from video sequences.

### V.4.5 Air losses

Bubbles from plumage and/or nostrils were observed in all recording sequences of both species. In all sequences, the number of bubbles lost from the birds was counted for each descent part of diving. Bubble volume at the moment of ejection from the bird ($V_{Bd}$) was calculated as: $V_{Bd} = 4\pi (0.5D_i)^3/ 3$, where $D_i$ is the bubble's diameter (m). $D_i$ of 82 bubbles and their respective ejection depth (m) were measured. To correct for hydrostatic pressure, in order to obtain a representative mean bubble volume at one atmosphere pressure, each bubble's volume was transformed as follows: $V_{Bs}=V_{Bd}[(\rho gd/P_{atm}) + 1]$, where $V_{Bs}$ is volume at sea surface, $\rho$ is the water density, g is gravity acceleration, d is depth and $P_{atm}$ is one atmosphere pressure in Pa. A representative average bubble volume at sea surface of $2.56 \times 10^7 (\pm 1.54 \times 10^{-8})$ m$^3$ ($0.256 \pm 0.015$ ml) was obtained. Air loss volume accumulated for each descent part of diving ($V_{Lost}$) was calculated multiplying the number of bubbles by $V_{Bs}$.

### V.4.5 Buoyancy, acceleration reaction and drag

Calculation of each bird's buoyancy required estimation of body volumes ($V_b$). For each live bird body volumes were extrapolated based on measurements from one dead individual of each species. It was deemed improper to sacrifice several birds to obtain a representative mean for $V_b$. Fortunately, there is a good linear correlation between $V_b$ and body mass ($m_b$) (Lasiewski and Calder, 1971). $V_b$ of the two dead individuals was determined by water displacement, following Lovvorn et al. (1991). $V_b$ was divided by $M_b$ to obtain a specific volume ($V_{sp}$) of $1.4018 \times 10^{-3}$ m$^3$ kg$^{-1}$ for Cassin's Auklet and $1.39 \times 10^{-3}$ m$^3$ kg$^{-1}$ for Xantus's Murrelet. Specific volume of both species was used to calculate $V_b$ for each bird tested ($V_{bi}= V_{sp} M_{bi,}$, where i represents each sampled bird). $m_b$ was adjusted for manipulated and control-manipulated birds by adding the respective vest mass.

Respiratory air volume ($V_L$) for each bird was calculated with the allometric equation from Lasiewski and Calder (1971) ($V_{lu} = 0.1608\ m_b^{0.91}$ liters). Units of $V_{lu}$ were transformed from liters to m$^3$. Volume of the body tissues ($V_T$) (water, protein, lipid and ash) was calculated following Lovvorn et al. (1999). Plumage air volume ($V_F$) was calculated as: $V_F = V_B - V_L - V_T$. Buoyancy force or upthrust ($F_{up}$) was calculated following Wilson et al. (1992) as: $F_{up} = \rho\ g\{[(P_{atm}\ V_{air})/(P_{atm} + \rho\ g\ d)] + V_T\} - m_b\ g$, where $V_{air}$ is the sum of the respiratory air volume and the plumage air volume, minus the volume of bubbles ($V_L + V_F - V_{Lost}$). Also, for manipulated trials $V_T$ included the volume of the vest's polyethylene material (4.02 x 10$^6$ m$^3$), and for control-manipulated trials $V_T$ included the total vest volume (3.8 x 10$^{-6}$ m$^3$).

Added mass ($M_a$) is usually ignored in wing-propelled divers that sustain an average speed relatively constant from one stroke cycle to the next, because negative inertial work during passive phases of the stroke cycle counteracts positive inertial work during active stroke phases (Bridge, 2004). $M_a$ is calculated as $\alpha \rho V_B$, where $\alpha$ is the added mass coefficient (Daniel, 1984). In the present study $M_a$ was included because the volume of the bird was reduced as a consequence of bubble loss. In a similar manner as done by Lovvorn and Liggins (2002), plots relating $\alpha$ to ratios of the three axes of an ellipsoid by Kochin et al. (1964) were used. Added mass coefficient was 0.1 for both alcids. The acceleration reaction was calculated as $G = -(m_b + M_a)\ a_y$, where $a_y$ is the vertical component of the diver's acceleration.

Drag for Cassin's Auklet was calculated as: $D = -0.206 + 1.28\ u - 0.267\ u^2 + 0.0914\ u^3$, where $u$ is the descent speed (Lovvorn et al., 2001). However, for Xantus's Murrelet there is not algorithm to estimate $D$. Thus, the same equation for drag of Cassin's Auklet was used for Xantus's Murrelet.

Power components $P_D$, $P_G$, $P_{up}$ were calculated multiplying the forces $D$, $G$ and $F_{up}$ per instantaneous descent speed, respectively. Work components $W_D$, $W_G$ and $W_{up}$ were calculated by integrating the respective power with time. Total work is $W_T = W_D + W_G + W_{up}$. Transport cost (COT) was estimated dividing $W_T$ by $m_b$ and by the vertical component of displacement (m s$^{-2}$). Finally to compare results from this contribution with those of other

studies, vertical descent speed, vertical displacement and work were calculated and reported in per flap cycle.

**V.4.6 Statistical analysis**

To test for the effects of buoyancy, a repeated-measures ANOVA was performed for both species on each of the diving performance parameters, with groups (control, manipulated, and manipulated control) as the within-subject factor. Data on 20 *P. aleuticus* individuals and 9 *S. hypoleucus* individuals were used in the repeated-measures ANOVA. Bonferroni post-hoc tests were used to identify significant differences. ANOVAs and post-hoc tests were carried out with SPSS v.12 (SPSS Inc., Chicago, IL, USA). In all statistical analyses, the probability level at which the null hypotheses of 'no difference' were rejected was $p > 0.05$. Henceforth, means are reported with their respective standard errors.

# V.5 Results

**V.5.1 Air losses**

No significant differences of bubbles lost, were found between experimental groups of each alcid species during diving (Auklet $F_{2, 38} = 1.58$, $p = 0.218$; Murrelet $F_{2, 16} = 1.59$, $p = 0.086$) (Table 3). As a first approximation, a second degree polynomial was fitted to mean air loss ($V_{Lost(t)}$, as bubbles) as a function of time, pooling together all diving sequences (due to the camera speed, a $V_{Lost(t)}$ mean was obtained every ~4 milliseconds). For Cassin's Auklet $V_{Lost(t)} = 3.8\,t^2 - 11.3\,t + 72$; with $r^2 = 0.9987$; and for Xantus's Murrelet $V_{Lost(t)} = 2.4\,t^2 - 9.8\,t + 68$, $r^2 = 0.9927$ (Fig. 11). Usually, bubbles were released from the plumage more rapidly during the beginning of the active flapping phase than during the rest of the cycle.
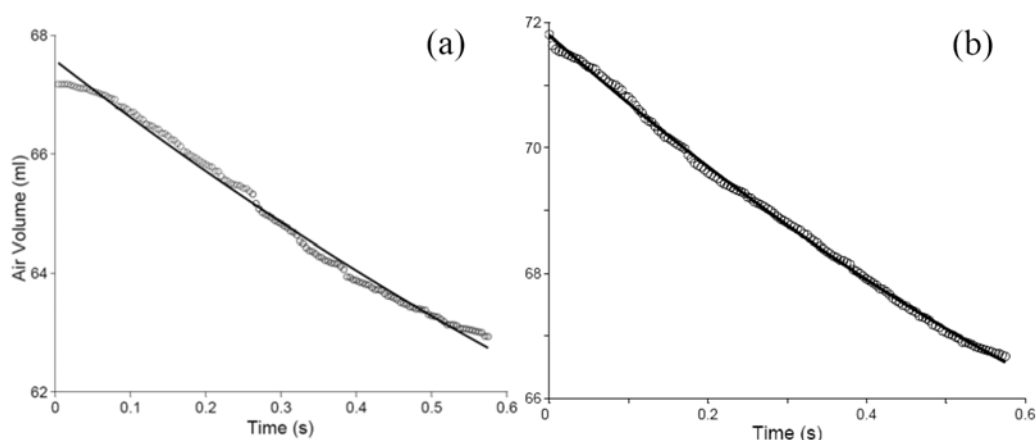
**Figure 11. Air volume reduction caused by the loss of air (bubbles) through time of diving. Each open dot represents the mean of air volume per frame (n = 60). Polynomial fit is represented by the solid line: For Auklet $V_{Lost(t)} = 3.8\ t^2 - 11.3\ t + 72$; with $r^2 = 0.9987$; and for Murrelet $V_{Lost(t)} = 2.4\ t^2 - 9.8\ t + 68$, $r^2 = 0.9927$, where $V_{Lost(t)}$ is the total air volume (ml) lost up to time t (s).**
**Figura 11. Reducción del volumen de aire producido por la pérdida de burbujas durante el buceo. Cada círculo en la gráfica representa la media del volumen de aire por cuadro en la secuencia de video (n = 60). La línea sólida representa el polinomio de ajuste: Para *P. aleuticus* $V_{Lost(t)} = 3.8\ t^2 - 11.3\ t + 72$; with $r^2 = 0.9987$; y para *S. hypoleucus* $V_{Lost(t)} = 2.4\ t^2 - 9.8\ t + 68$, $r^2 = 0.9927$, donde $V_{Lost(t)}$ es el volumen total de aire perdido (ml) hasta el tiempo t (s).**

*Table 3 Dive parameters. Mean data ± SE.*
*Tabla 3. Parámetros de buceo. Media ± error estándar*

| Parameters | Cassin's Auklet (n=20) | | | Xantus's Murrelet (n=9) | | |
|---|---|---|---|---|---|---|
| | Control | Manipulated | M. Control | Control | Manipulated | M. Control |
| **Speed (m s$^{-1}$)** | 0.77±0.027 | 0.53±0.018 | 0.70±0.020 | 0.67±0.03 | 0.53±0.04 | 0.67±0.03 |
| **Displacement per flan (m)** | 0.231±0.007 | 0.185±0.008 | 0.225±0.007 | 0.19±0.01 | 0.14±0.01 | 0.20±0.01 |
| **Flap duration (s)** | 0.315±0.008 | 0.363±0.011 | 0.336±0.006 | 0.30±0.02 | 0.28±0.01 | 0.30±0.02 |
| **Work per flan (J)** | 0.31±0.02 | 0.23±0.01 | 0.29±0.02 | 0.23±0.01 | 0.15±0.02 | 0.23±0.02 |
| **Drag/Buoyancy ratio** | 1.22±0.06 | 0.67±0.03 | 1.1±0.04 | 1.13±0.05 | 0.74±0.06 | 1.07±.07 |
| **Num. of Bubbles loss** | 24.9±1.3 | 22±0.9 | 22.3±1.4 | 20.33±1.29 | 19.67±1.47 | 19.56±1.56 |
| **Transport cost (J kg$^{-1}$m$^{-1}$)** | 8.73±0.4 | 7.97±0.2 | 8.29±0.26 | 7.82±0.28 | 6.62±0.55 | 7.41±0.59 |

**V.5.2 Diving behavior**

Foot propulsion was observed in all recorded sequences of Xantus's Murrelet, but only in some of the sequences of Cassin's Auklets. Usually murrelets alternated left and right foot thrusts during diving in any part of the flapping cycle; whereas, auklets synchronized the stroke of both feet with the active downstroke of wings.

**V.5.3 Diving performance**

Repeated measures ANOVA analysis revealed a significant effect in speed of manipulated birds for each specie (Auklet $F_{2, 38} = 33.85$, $p<<0.001$; Murrelet $F_{2, 16} = 9.76$, $p = 0.002$) (Fig. 12a), as well as displacement per flap (Auklet $F_{2, 38} = 10.20$, $p<<0.001$; Murrelet $F_{2, 16} = 13.45$, $p<<0.001$) (Fig. 12c) and work per flap (Auklet $F_{2, 38} = 6.587$, $p = 0.004$; Murrelet $F_{2, 16} = 6.274$, $p = 0.01$) (Fig 12d). No significant effect was found in the cost of transport of manipulated birds (Auklet $F_{2, 38} = 1.65$, $p = 0.205$; Murrelet $F_{2, 16} = 1.67$, $p = 0.22$) (Fig. 12e). Significant effect was found in the flap duration of manipulated auklets ($F_{2, 38} = 10.04$, $p<<0.001$), but it was not significant for murrelets ($F_{2, 16} = 0.57$, $p = 0.58$) (Fig. 12b).

For both alcid species, the increased buoyancy treatment decreased displacement per flap, drag/buoyancy ratio, and work per flap compared to both controls, (Bonferroni test, $p<0.01$ for all test of both alcids). Manipulated auklets showed lower flap duration than controls (Bonferroni test, $p = 0.001$), but those for murrelets were not significantly different (Table 3).
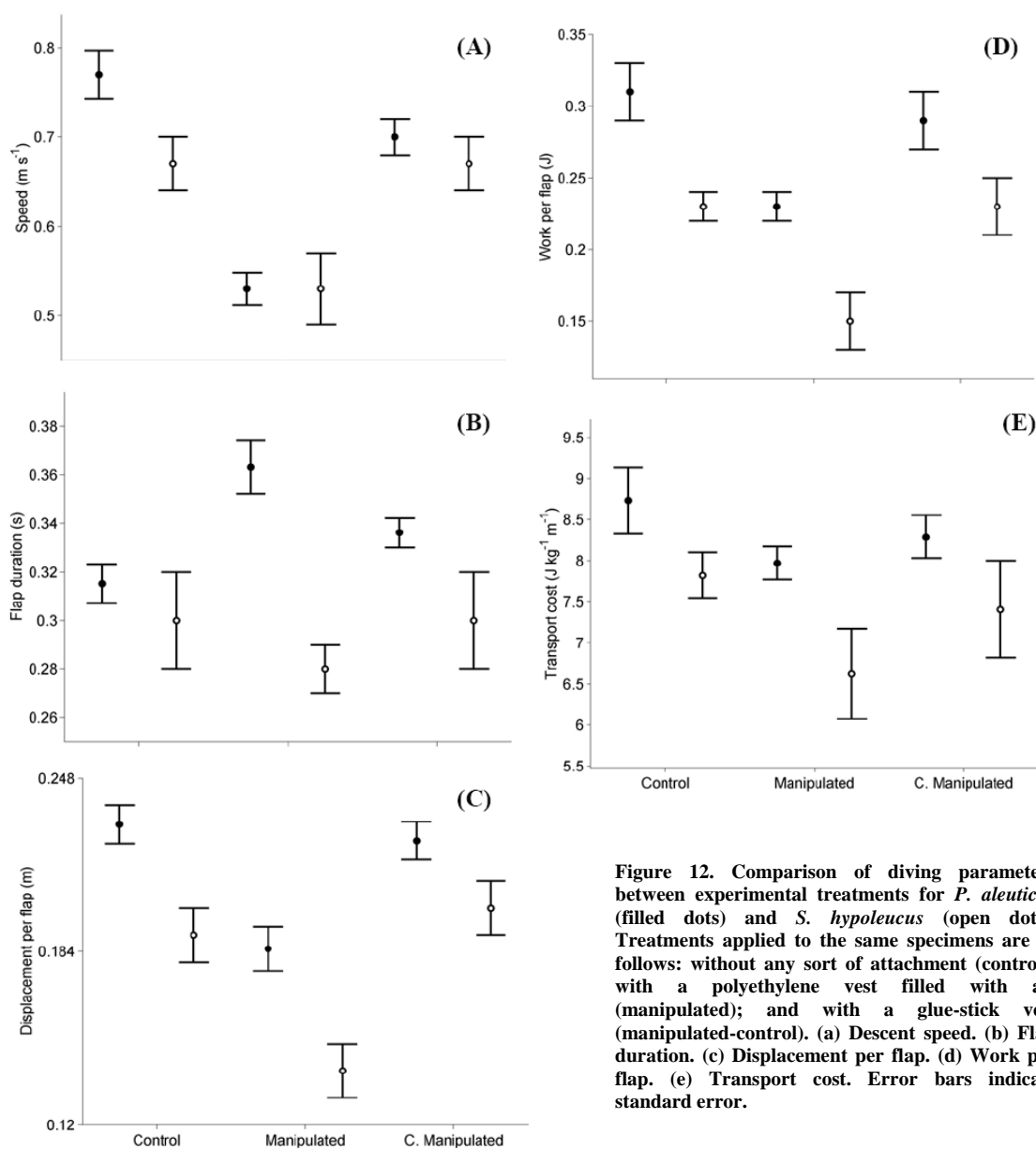
Figure 12. Comparison of diving parameters between experimental treatments for *P. aleuticus* (filled dots) and *S. hypoleucus* (open dots). Treatments applied to the same specimens are as follows: without any sort of attachment (control); with a polyethylene vest filled with air (manipulated); and with a glue-stick vest (manipulated-control). (a) Descent speed. (b) Flap duration. (c) Displacement per flap. (d) Work per flap. (e) Transport cost. Error bars indicate standard error.

Figura 12. Comparación de los parámetros de buceo entre los tratamientos experimentales para *P. aleuticus* (símbolos cerrados) y *S. hypoleucus* (símbolos abiertos). Los tres tratamientos aplicados a los mismos especimenes fueron los siguientes: Sin ningún tipo de chaleco (control); cargada con un chaleco de polietileno de baja densidad lleno de aire (manipulado); y con un chaleco de silicón con flotabilidad neutra (control-manipulado). (a) Velocidad de descenso. (b) Duración de aleteo. (c) Desplazamiento por aleteo. (d) Trabajo por aleteo. (e) Costo de transporte. Las barras indican los errores estándares.

# V.6 Discussion

## V.6.1 Air losses

Results from this work suggest that the rate of air loss decreases progressively with time, as suggested by Stephenson (1994). During dives down to 1.5 m deep, Lesser Scaup lose 19% of the initial air volume from both plumage and respiratory system (Stephenson, 1994, 1995). Stephenson (1994) assumed a constant loss rate (7.8 ml $s^{-1}$) of air plumage during descent and feeding. He indicated that this rate could not continue indefinitely, because ducks would empty their plumage air content in 34 s of submergence, and because empirical evidence indicates that ducks dive for longer than 34 s without becoming wetted. For both alcids studied, the resulting equation indicates a maximal air volume loss of ~12% with respect to initial content at ~1.5 s of diving, a percentage smaller than that reported by Stephenson (1994). Note that these estimations did not take into account the volume changes with depth. Indubitably bubbles are discrete entities, although to develop the equation to estimate air loss as a function of time, continuity was assumed for the variables. Bubbles were more common during active flap phases than during the passive ones. This observation could be appreciated in the 'wave behavior' of data points around the fitted curve (Fig 1). Methods used in the present study to identify and count bubbles through time could possibly underestimate total volume because video quality could not help to detect very small bubbles (<0.2 ml). But, it is reasonable to assume that the contribution of these small bubbles was negligible. Thus, these results suggest that both alcids lose a smaller volume of air than ducks, when diving. Possibly this difference is because the duck's feathers differ in their microstructure and they have a lower resistance to water penetration than the feathers of alcids (Rijke, 1970), promoting a greater loss of air from plumage in the former.

The release of bubbles during diving could represent an important cost, because heat conduction depends on the plumage's air volume fraction. Heat transfer model applied to penguin feathers suggests that the air layer thickness and afterfeather length are responsible

for the insulation of the bird (Dawson et al., 1999). Possibly, the maximum loss of air from plumage of penguins, and similar diving birds, depends inversely on the capacity of afterfeathers to be compressed. Small size alcids have larger afterfeathers than those of storm-petrels (Ortega-Jiménez et al., 2009). The large size of afterfeathers of alcids possibly serves to reduce both heat and air losses during diving.

## V.6.2 Buoyancy, speed and diving performance

When their buoyancy was experimentally increased, the birds reduced their descent speed by 31% and 21% for auklets and murrelets, respectively. These results suggest that the loss of air volume from plumage and/or respiratory system could improve the descent speed of diving birds. Lovvorn et al. (1999) predicted theoretically that the distance per stroke and resulting speed would increase as buoyant resistance decreased, if the flap duration and work per flap remained constant throughout descent. The details of the effects of buoyancy reduction on diving performance as measured in this work's experiments are not explained by Lovvorn et al.'s (1999) model, because this model does not include the discrete loss of bubbles. The model partially explains the positive effect on descent speed. However, it is not proper to apply this model to data from this work, because the energy per flap and flap duration was affected.

The cost of transport of manipulated birds apparently decreases as a consequence of the buoyancy increment (Fig. 12). However significant differences were not found. The observed diving speed changes could have resulted from the minimization of the cost of transport as a consequence of the air volume load (or loss). In contrast, studies with other species of medium size alcids resulted in relatively constant swimming speed during descent (Lovvorn et al., 1999; Watanuki et al., 2006). In these cases, Lovvorn et al.'s (1999) model failed to predict speed. This failure could be due to the model not taking into account air losses from plumage and respiratory system during the first meter from sea surface. Thus, a new model is needed where energy per flap and flap duration are allowed to change while the cost of transport remains constant. Also, the inclusion of the near sea surface loss of air volume, in the new model, could make it possible for the birds to reach

close to maximal speed in the early stages of descent diving. The construction of this new model is beyond the scope of the present work but could be achieved in future work.

The difference between drag/buoyancy ratio for manipulated and non-manipulated birds, could be explained by the exponential increase of drag force with speed (Lovvorn et al., 2001). Descent speed is larger for non-manipulated birds and this increases drag force. Lovvorn and Liggins (2002) modeled the work per stroke for steady horizontal diving of Cassin's Auklet (without buoyancy component), and they found a cost of transport of $6 \, J \, kg^1 \, m^{-1}$. This value is smaller than the one resulting from the present study ($8.7 \, J \, kg^{-1} \, m^{-1}$). This difference is expected because for diving birds buoyancy represents important costs for their underwater motion.

### V.6.3 Foot propulsion and motivational state

Motivational state is an important factor in short-burst motion behavior and performance. Escape-state motivation results in a narrow margin of behavioral choices, hence, 'escape' divings are suitable for comparative studies, where maximal or quick responses are needed. However, a strong motivation could induce intense behavioral responses if the goal for the birds is to escape.

Video recordings suggest that foot propulsion could improve diving performance of both alcids. In the present study, the cost of foot-propulsion was not quantified, because it would require a comparison of wing-foot propulsion with wing propulsion only, in the same specimens. This could be done in future work. Richman and Lovvorn (2008) found that diving performance of the White-winged Scoter was increased (e.g., higher speed and distance per stroke) when both wing and foot were used for propulsion than when ducks used their feet only. Possibly, the increase in flap duration observed in manipulated auklets could be attributed to foot propulsion.

**V.6.4 Ecological implications**

Results from this study suggest that air lost as bubbles may improve descent speed during diving of small size alcids. Auklets and murrelets feed on euphausiids and epipelagic schooling fishes (Hodum et al., 1998; Hamilton et al., 2004). These birds demonstrate a maximum diving duration of up to ~50 s with a mean of 30 s (Watanuki and Burger, 1999). If we assume that maximum diving duration of descent and ascent are 25 s each, air loss could increase the total depth reached by the bird from 13 m to 19 m for Cassin's Auklet and from 13 to 17.5 for Xantus's Murrelet (Table 3).

# Chapter VI

## Future work

## VI.1 Proposals

Thermal conductance measurements of dry and apparently wet plumage of alcids are needed to test if one-side wet feathers contribute to reduce heat loss during prolonged diving.

A solid substrate is lacking for birds at sea, and leg thrust is either not used or of little use. Takeoff measurements from the sea surface are needed to understand the role of leg trust.

Headwinds can greatly facilitate takeoff (Pennycuick, 1978), and Storm-petrels may be better able to exploit these when taking off, due to their low wing loading and relatively large wingspan. Experiments designed to evaluate benefits of headwinds at different speeds and angles are needed.

Measurements of maximum lift production in a representative number of seabirds are needed to test Marden's (1990) predictions about the relation between maximal lift and muscle mass. Marden (1990) used ten species of terrestrial birds.

A new model is needed where energy per flap and flap duration are allowed to change while the cost of transport remains constant. Also, the inclusion of the near sea surface loss

of air volume could make it possible for the birds to reach close to maximal speed in the early stages of descent diving.

The cost of foot-propulsion for alcids could be quantified with experiments comparing wing-foot propulsion during diving with wing propulsion only, in the same specimens.

# Chapter VII

## Conclusions

- One-side wet feathers of both alcids resisted an air pressure of 1.25 kPa, but dry feathers did not resist any pressure in excess of atmospheric pressure for air penetration.

- One-side wet feathers promote partial plumage wettability without increasing water penetration significantly, compared with dry feathers: $P_w$ for Xantus's Murrelet was 1.47 kPa and it was 1.36 kPa for Cassin's Auklet.

- Plumage wettability had a negative effect on takeoff performance of the three studied species. *P. aleuticus* and *S. hypoleucus* retained less water than *O. leucorhoa*. But this difference is explained by *O. leucorhoa's* surface to volume ratio larger than that of the alcids. Feather architecture and afterfeather-feather length ratio ($r_f$) differed between both alcids and *O. leucorhoa.* Possibly, in alcids the large afterfeathers help to reduce heat loss during diving.

- Mean maximum extra load supported by Leach's storm petrels was 45% of body mass, 23% by Cassin's Auklet, and 21% by Xantus's Murrelet. Mean maximum induced power output was 0.7 W for Leach's Storm-petrel, 4.5 W for Cassin's Auklet, and 5.7 W for Xantus's Murrelet.

- All specimens had a smaller descent speed during diving when loaded with an artificial air vest. Drag cost was higher than buoyancy in non-manipulated birds. The air volume loss measured during diving down to 0.7 m depth was 9% and 8% of the total air volume of Cassin's Auklet and Xantus's Murrelet, respectively. But, for both alcids the maximal loss of air estimated from a regression model indicated a 12% loss with respect to initial air volume at ~1.5 s of diving. Foot propulsion was observed in all record sequences of Xantus's Murrelet, but for Cassin's Auklets it was only observed in some of the recorded sequences. Experimental results suggest that the air loss could improve the descent speed during diving in small size alcids increasing their feeding opportunities.

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