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TIDAL AND INSIDE-SEASON EFFECTS ON THE DIVING BEHAVIOR OF PELAGIC CORMORANTS (*Phalacrocorax pelagicus* Pallas, 1811) AT CATTLE POINT, SAN JUAN ISLAND, WASHINGTON, U.S.A.

EFECTOS DE LAS MAREAS Y DE LOS PERÍODOS INTRA ESTACIONALES EN EL COMPORTAMIENTO DE LOS CORMORANES PELÁGICOS (*Phalacrocorax pelagicus* Pallas, 1811) DURANTE EL BUCEO EN CATTLE POINT, SAN JUAN ISLAND, WASHINGTON, U.S.A

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Abstract

The influence of time of day, tidal depth, current and inside-season change on the diving behavior of pelagic cormorants, as well as the relationships between diving time and the preceding and the subsequent surface time were examined at Cattle Point, San Juan Island. Diving behavior was recorded using focal animal sampling. Dives and surfaces were timed to the nearest second. Correlations between dive time and the other variables were analyzed using regression analysis and *t*-test of significance. On a daily basis, dive times varied with time of day, tidal depth and current direction. Dive times were longer later in the day, showing a trend to be longer when height of the tide was higher and during ebb tides. However, dive times remained variable throughout the course of the season. No inside-season related variation on diving times was found, probably due to changes in prey availability. Mean dives and recovery times were 31.2 sec and 19.1 sec respectively showing that dive times were longer than surface times. Even so, positive relationships were found between dive time and the preceding surface time and between dive time and the subsequent surface time suggesting that cormorants utilize both anticipatory and reactive breathing according to the foraging environment.
Key words: pelagic cormorant, diving time, resting periods, anticipatory breathing, reactive breathing, tidal depth, ebb tide, flood tide.

Resumen

En Cattle Point, San Juan Island, se investigó la influencia de la hora del día, la profundidad de la marea, las corrientes y la variación intra estacional en el comportamiento durante el buceo en cormoranes pelágicos, así como la relación entre la duración del buceo y los tiempos en la superficie previos y posteriores al mismo. Para registrar la duración del buceo se utilizó un muestreo dirigido. La duración del buceo se midió en segundos y se utilizaron la prueba de t y análisis de correlación para investigar la relación entre su duración y demás variables. Se encontró que la duración del tiempo de buceo variaba con la hora del día, la profundidad de las mareas y la dirección de las corrientes. Los buceos eran de mayor duración en horas vespertinas, tendiendo a ser más prolongados cuanto mayor fuera la profundidad del mar y durante la marea entrante. Los tiempos de buceo fueron variables durante la estación y no se encontraron diferencias intra estacionales, posiblemente debido a influencias en la disponibilidad de presas. La duración promedio de los buceos fue de 31.2 s y los tiempos de recuperación de 19.1 s, es decir que los buceos duraron más que los tiempos en la superficie. Se encontraron relaciones positivas entre la duración del buceo y el tiempo previo al mismo, así como entre la duración del buceo y el tiempo posterior en la superficie. Esto sugiere que los cormoranes utilizan una respiración anticipatoria y reactiva frente al ambiente de forrajeo.
Palabras clave: cormorán pelágico, duración de buceo, períodos de descanso, respiración anticipatoria, respiración reactiva, profundidad del mar, marea baja, marea alta.

Introduction

The San Juan Archipelago is a complex, dynamic and rich marine ecosystem in which a great number of marine organisms live, from species of plankton to marine mammals. This complexity is due to environmental factors as well as strong stream flows and oceanic influences. This ecosystem with high fish and plankton abundance favors the presence of numerous species of seabirds such as the Pelagic Cormorant (*Phalacrocorax pelagicus*).

Cormorants are foot propelled pursuit divers that forage inshore (Ashmole, 1971; Cooper, 1986;

Sapoznikow & Quintana, 2003; Gaston, 2004; Wanless *et al.,* 1992; Punta *et al.,* 1993) and have exceptional diving abilities (Croxall *et al.,* 1991; Wanless, 1995). These birds typically alternate relatively short periods of active foraging fairly close to land with long periods of resting ashore or on water (Wanless & Harris, 1991).

Like other avian divers, their diving performance is affected by different environmental variables such as water depth, bottom substratum and prey density due to food accessibility is directly related to these factors (Sapoznikow & Quintana, 2003; Croll *et al.,* 1992; Hustler, 1992). Seasonal patterns affect fish abundance (Kato *et al.,* 2001), so it can be expected that behavior of piscivorous birds is affected as well. Furthermore, according to some physiological constraints, long dives should be followed by long resting periods, in order to restore oxygen supplies (Cooper, 1986; Lea *et al*., 1996; Jodice *et al.,* 1999; Wanless *et al*., 1992). In this way, it would be expected to have longer dives during higher tidal depths due to demersal species being deeper in the water and that cormorants follow the 1:1 of dive time to surface time showed by other diving birds (Kooyman & Ponganis, 1997).

In this study, the time of the day and factors such as tidal depths and currents, as well as the inside-season influence on the diving behavior of Pelagic Cormorants were examined. Relationships between dive time and either the preceding or subsequent surface times as different breathing strategies were also investigated.

Methods During October and November 2004, diving behavior of Pelagic Cormorants was observed at Cattle Point, San Juan Island (Figure 1).

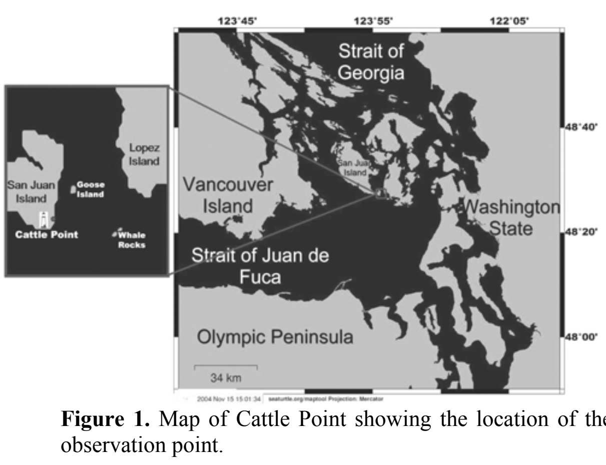


Figure 1. Map of Cattle Point showing the location of the observation point.

Specifically, we measured the length of time that birds were submerged and how long they remained on the surface between dives using the "focal animal sampling" method (Altmann, 1974). Times of diving and reemerging were recorded to the nearest second. We followed each focal bird as long as possible from its detection until the bird flew away, swam too far out to be observed; disappeared from view; or when it joined up with another bird so it became difficult to identify which bird had surfaced. Observations were done using binoculars or with the naked eye.

For each sampling event, we recorded date, time, weather, tide height plus current direction and speed. We also noted weather a fish or another prey item was brought to the surface. Data were collected by two people, one performing the observations and the other one recording the information to avoid losing site of the bird.

Regression analysis and *t*-test of significance ($\alpha = 0.05$) were used to analyze the relationships between dive time and the other variables.

Results

A total of 40 Pelagic Cormorants feeding bouts were observed in this study. From these, 891 dives and surfaces were analyzed. Dive times ranged from 7-87 seconds. Mean dive time was 31.2 $\pm$ 11.7 s. Surface times were shorter than dives and more variable in duration, having a higher standard deviation. Surface times ranged from 6-90 seconds and the mean was 19.4 $\pm$ 12.1 s.

Daily patterns

On a daily basis, a strong correlation between dive time and time of day was found ($P < 0.0001$). Figure 2a shows dives were longer as the day progressed. This strong correlation may be affected by the state of tide and currents as well.

Tidal depth affected diving behavior of cormorants, such that dives were longer when the height of the tide was higher ($P = 0.0362$). However, some of the dives were longer and shorter than the trend (Figure 2b), indicating that the cormorant's dive was affected by other factors. There was also a clear tidal current effect. During ebb tides, dive times increased as current increased ($P = 0.0003$). On the other hand, during flood tides dives decreased as current increased ($P = 0.0049$ respectively) (Figure 2c).

Inside-season

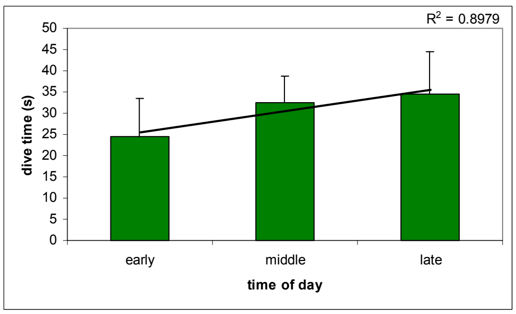
Overall, dive time did not change significantly throughout the course of the season (fall). Dives remained variable not showing a clear trend ($P = 0.8688$) (Figure 3). This result suggests that prey availability may not be influencing diving behavior of cormorants or prey abundance did not change.

Dive and surface time relationships

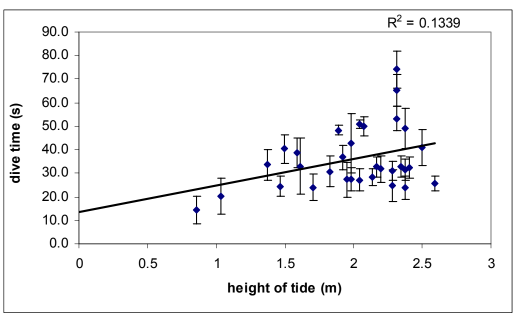
Cormorants dive were twice as long as surface times in some cases and for others were almost five times longer than surface times, going against the 1:1 of diving time to surface time expected for other diving birds (Kooyman & Ponganis, 1997). The latter means that the longer a diving animal stays underwater, the longer it must stay on the surface between dives in order to restore its oxygen supplies (Dewar, 1924).

Figure 2. Daily variation of dive time related to time of day (a), height of the tide (b) and current velocity and direction (c).

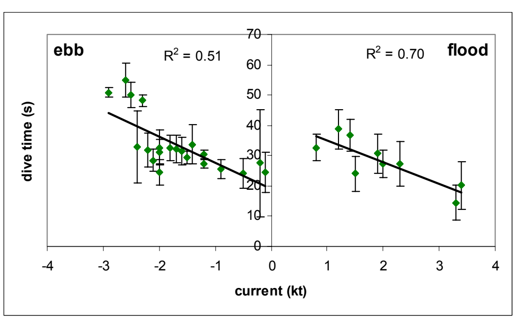
a. Means of dive time with time of day (early 0900-1200, middle 1200-1400, late 1400-1700).



b. Means of dive time and in relation to height of the tide.



c. Ebb and flood tides effect.



Regression plots of dive and surface times showed a number of outliers, especially in surface times. The longest surface times were recorded when the birds brought prey items to the surface, probably because prey were too big to be swallowed under water. These outliers were deleted from the data set to avoid distortion of the trends. Dive and surface intervals were correlated for each bird to find out if either the preceding or the subsequent surface time was better related to the dives. These relationships were examined thoroughly comparing the regression coefficients using *t*-tests. Twenty bouts (50%) had a positive relationship with the subsequent surface time ($P = 0.0026$), nineteen (47.5%) of them had a positive relationship with the preceding surface time ($P < 0.0001$), and one bout (2.5%) showed no correlation at all ($r = 0.00004$) (Figure 4).

Figure 3. Inside-season change of dive time.

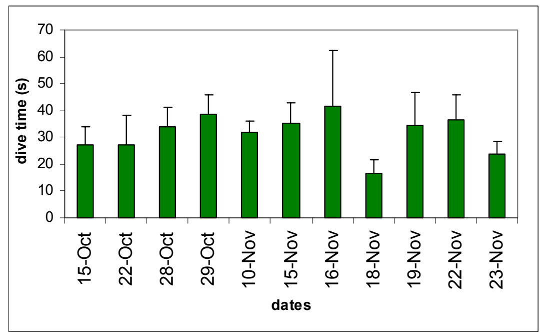
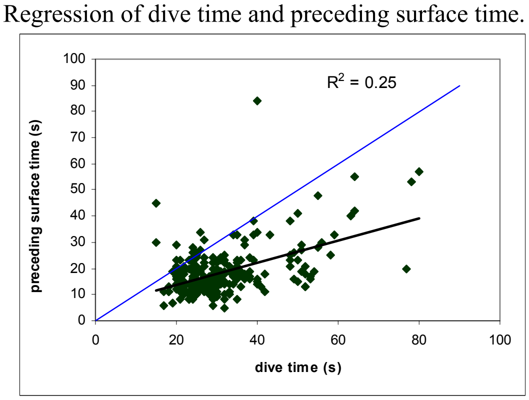
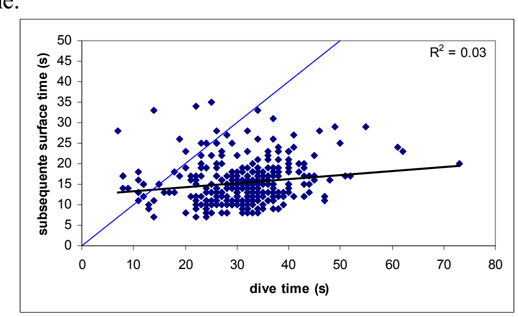


Figure 4. Positive relationships between dive time and the preceding surface time (a) and the subsequent surface time (b). Blue lines show the predicted 1:1 of dive time to surface time.

a. Regression of dive time and preceding surface time.



b. Regression of dive time and subsequent surface time.



Discussion

Daily variation and other factors affecting diving time

According to Dorfman & Kingsford (2001) cormorants show diel feeding patterns. Furthermore, availability of prey may change with time of day and this could then affect diving behavior of cormorants. Thus longer dives later in the day may be a response to lower prey abundance.

Cormorants diving behavior may also be related additionally to other factors such as tidal depth and currents. Water depth and tidal cycle influences cormorant diving behavior (Sapoznikow & Quintana, 2003; Dorfman & Kingsford, 2001; Jodice *et al*., 1999; Richne, 1995; Croll *et al*., 1992). A positive relationship between dive time and height of the tide would be explained by the fact that during high tides cormorants have to dive deeper. Even so, we found moderate number of dives under the trend (Figure 3b), suggesting that cormorants were feeding on epipelagic schooling fish instead of demersal species, therefore capturing prey in shallow waters during high tides. Hence changes in dive times could be related then to differences in prey distributions within the water column.

With respect to currents, birds foraging close to shore with ebb and flood tides may benefit from tidal upwelling or tidal eddies (Irons, 1998). According to Dorfman & Kingsford (2001) and Richner (1995), who studied cormorants in Australia and Scotland respectively, cormorants feed more frequently during ebbing tides. However Zamon (2003) found in the San Juan Island area that prey is more available during flood tides. Thus birds are expected to have shorter dives during the floods, when the incoming current is bringing more prey, and longer dives during the ebbs, when the outgoing current is taking away the food available (Figure 3c). Therefore current direction is affecting diving times more than current velocity.

Inside-season effect on diving time

The lack of inside-season-related variation may be attributed to patterns in prey availability. Cormorants feed actively on demersal species such as sand lance (Kato *et al*., 2001). Sand lance are a stationary species (Zamon, 2003) that spend most of the winter buried in the sand rarely being caught in the water column (Robards & Piatt, 1999). According to Robards and Piatt (1999), several reports allude the possibility that sand lance migrate to deeper waters during winter. Due to these reasons, it could be expected that cormorants would dive longer to find prey throughout the season. However, given that cormorants are opportunistic feeders (Kato *et al.,* 2001; Dorfman & Kingsford, 2001), they may also feed on epipelagic schooling fish when they are more available. Flexibility in prey choice may explain why inside-season change is not directly affecting diving behavior.

The dive-surface relationship

Comparative data on duration of dives and recovery periods on the surface between dives, suggests that different bird species may allocate their time in different ways depending on their foraging ecology (Wanless *et al*., 1992). Here cormorants demonstrated different dive-surface time relationships. A positive relationship between a dive and the preceding surface time suggests that the birds remain on the surface for a period of time prior to the dive loading their oxygen stores and will dive until their oxygen stores are depleted, this is called anticipatory breathing. On the other hand, a positive relationship between a dive and the subsequent surface time suggests that birds emerged from their dive and remain on the surface filling up again their oxygen stores; this is called reactive breathing (Lea *et al.,* 1996). In this study the correlation coefficient for each of these relationships was not very strong. Dive times showed a weak dependence on surface time implying that birds store oxygen from one dive to another, presumably as Lea *et al.,* (1996) found because the oxygen stores were not close to be depleted during the dive. A reason for this is that cormorants select either anticipatory or reactive breathing depending on the features of the foraging environment.

In conclusion, on a daily basis, dives were affected not only by time of day, but tidal depth, direction of the current, and probably prey availability. Diving behavior of pelagic cormorants did not change over the course of the season. However, this study was very short and in a year long research study a season-related variation might be found. Regarding the dive-surface relationship, pelagic cormorant utilize both the preceding and the subsequent breathing as feeding strategies according to the environment that surrounds them. Further research involving a larger sample size, longer temporal scale, and new variables such as water depth, prey availability, and diet may be used to confirm these results.

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