Behavior of Risso's Dolphins (*Grampus griseus*) in the Southern California Bight: An Aerial Perspective

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Abstract

Risso's dolphin (Risso's; *Grampus griseus*) behavior is little described given their typical offshore distribution where research access is inherently challenging. We conducted focal group behavior follows of 51 Risso's groups from a circling, small, fixed-wing Partenavia aircraft in the Southern California Bight from 2008 through 2012 (15 aerial surveys; 72,647 km; 86 d). Instantaneous scan sampling of group heading and behavior state (rest/slow travel, medium-fast [mf] travel, and mill), and maximum nearest neighbor distance (MNND) estimated in adult body lengths (BLs) were noted once per 30 s. Focal follows occurred for 5 to 59 min ($n = 51$, mean 21.6, standard deviation [SD] = 12.9). Mean group size was 25.8 ($n = 51$, SD ± 23.62, range 3 to 120). A total of 1,446 usable headings, 1,275 MNND, and 1,359 behavior state data points were used to calculate response variables of reorientation, splitting-joining, and behavior state transition rates relative to explanatory variables using standard multiple-linear-regression, logistic regression, or multinomial logistic regression models. Reorientation rates tended to be higher when other species were present. No explanatory variables were found to influence the splitting-joining rate. Risso's behavior state was significantly affected by calf presence and time of day. Risso's groups spent most (60%) time engaged in rest/slow travel followed by mf travel (33%) and milling (7%), and rarely changed behavior state. Transitions from one behavior state to another were more common in groups with calf presence, which were 4.3 times more likely to continue mf travel than non-calf groups. During early afternoon, Risso's were six times more likely to continue mf travel versus early morning and late afternoon. Preponderance of daytime rest/slow travel likely reflects presumed need for diurnal rest prior to apparent nocturnal foraging, a pattern associated with other nocturnal foraging dolphin species. Observations from aircraft facilitate a unique bird's eye view on social interactions and spacing of individuals, which are less available from the low-vantage perspective of other platforms.

Key Words: Risso's dolphin, *Grampus griseus*, behavior state, reorientation rate, nearest neighbor distance, inter-individual distance, sequential behavior, focal group follow

Introduction

Risso's dolphins (*Grampus griseus*; hereafter simply "Risso's") preferentially inhabit temperate and tropical shelf-edge/continental slope waters (depth 200 to 1,000+ m) typically associated with offshore pelagic areas (Baird, 2009; Bearzi et al., 2010; Jefferson et al., 2014b, 2015; Hartman, 2018). Data on their behavior and group characteristics have been collected from a few locations in nearshore waters characterized by steep coastal slope drop-offs and relatively high biological productivity (e.g., Baird, 2009; Jefferson et al., 2014b, 2015). Such areas include Monterey Bay (Kruse, 1989; Kruse et al., 1999) and Santa Catalina and San Clemente Islands off California in the United States (Shane, 1994, 1995a; Henderson, 2010; Soldevilla et al., 2010, 2011; Smultea & Jefferson, 2014; Smultea, 2016; Smultea & Lomac-MacNair, 2016), the Azore Islands of Portugal (Hartman et al., 2008, 2014, 2015; Visser et al., 2011; Hartman, 2015), and the Mediterranean Sea (Bearzi et al., 2010).

The Risso's dolphin is a medium-sized (~3 m body length) delphinid (Figure 1) presumed to

Figure 1. A group of Risso's dolphins (*Grampus griseus*) photographed in the study area on 2 February 2012 by B. Würsig under NMFS permit 14451. White line indicates how maximum nearest neighbor distance (MNND) was estimated for a group (in this case, rounded to two body lengths).

consume primarily cephalopods, particularly meso-pelagic squid, based on reduced dentition and a few stomach samples (Clarke & Pascoe, 1985; Würtz et al., 1992; Shoham-Frider et al., 2002; Blanco et al., 2006; Bearzi et al., 2010; Jefferson et al., 2015). A comprehensive review reported typical group size of approximately 15 to 20 dol-phins (Jefferson et al., 2014b). The most detailed long-term studies of Risso's come from vessel- and shore-based research in the Azore Islands that include individual photo-identification and genetic sampling. Associated data indicate habitat segrega-tion by age and sex, some mid- to long-term indi-vidual associations primarily among adult males and females, and some site fidelity with relatively restricted home ranges (Hartman et al., 2008, 2014, 2015; Hartman, 2015, 2018). Genetic analysis of Risso's in the Ligurian Sea revealed low levels of relatedness with the exception of females (Gaspari et al., 2004). In addition, genetic data collected and animals killed in a Japanese fishery led to the hypothesis that mature males may move among groups (Baird, 2009).

Risso's in the Southern California Bight (SCB) belong to the California/Oregon/Washington stock inhabiting shelf, slope, and offshore waters (Forney & Barlow, 1998; Carretta et al., 2017). Year-round aerial surveys indicate that this stock occurs most commonly off California during the winter months and then shifts northward to Oregon and Washington waters during the late spring and summer (Green et al., 1992; Forney & Barlow, 1998; Carretta et al., 2017). The abun-dance and distribution of Risso's is known to vary with changes in seasonal and inter-annual oceanographic conditions (Forney & Barlow, 1998; Bearzi et al., 2010; Campbell et al., 2015). In the SCB, Risso's abundance has been increas-ing over the last few decades, before which they were considered relatively rare (Leatherwood et al., 1980; Shane, 1995a; Forney & Barlow, 1998; Carretta et al., 2000, 2017; Jefferson et al., 2014a; Smultea & Jefferson, 2014). Their influx was correlated with the apparent near abandon-ment of SCB waters by short-finned pilot whales (*Globicephala macrorhynchus*) in the early 1980s. This shift in species abundance has been attrib-uted to a concomitant severe El Niño Southern Oscillation and decrease in squid abundance (Barlow, 1995; Shane 1995a), live captures of an estimated 78 pilot whales for aquaria, fishery bycatch, and intentional shooting by fishermen (Jefferson & Schulman-Janiger, 2018), as well as potential inter-specific aggressive and com-petitive displacement (Shane, 1995b). Pilot whale sightings are still considered rare to the SCB,

while Risso's are now the second-most common species of cetacean there (Douglas et al., 2014; Jefferson et al., 2014a; Smultea & Jefferson, 2014; Campbell et al., 2015). This historical shift in abundance between the two species is still not well understood.

There is little information on group behavioral patterns of Risso's regarding behavioral budget, group cohesion and inter-individual spacing, and orientation, particularly in the SCB. Near Santa Catalina Island in the SCB (Figure 1), Shane (1995a) reported that Risso's primarily traveled (84% of 234 instantaneous observation samples), with feeding observed only three times (1% of the samples), and other behavioral states similarly rare. Most travel (57%) occurred at regular speed, with 41% at a slow travel speed that Shane (1995a) interpreted as an aroused type of resting. Kruse (1989) similarly reported that Risso's in Monterey Bay off central California predominantly traveled. Typical group sizes for Risso's off California range from about 10 to 50 individuals (Forney & Barlow, 1998; Carretta et al., 2000; Jefferson et al., 2014a, 2014b; Smultea, 2016), and they are often associated with other marine mammal species (Smultea et al., 2014; Smultea, 2016; Bacon et al., 2017). Some of these inter-specific interactions appear to be aggressive and include charging and breaching on sperm whales (*Physeter macrocephalus*; Smultea et al., 2014), circling northern right whale dolphin (*Lissodelphis borealis*) mother–calf pairs (Smultea, 2016; Bacon et al., 2017), and charging common bottlenose dolphins (*Tursiops truncatus*; Shane, 1994). Other inter-specific interactions appear to be neutral or social such as swimming, with little change in behavior and intermingling of individuals of different species (Smultea, 2016; Bacon et al., 2017). Given the paucity of information available on the behavior and ecology of Risso's, additional data are needed on their natural history and how their management and conservation might be affected by ongoing anthropogenic factors. Such activities in the SCB include military training involving mid-frequency active sonar (MFAS) and underwater detonations, shipping, tourism, and fishing via entanglement and competition for Risso's primary squid prey.

The importance of studying animal behavior in the context of identifying potential adverse impacts of anthropogenic activities is a growing discipline in the field of conservation behavior. This approach includes identifying behavioral responses to potential stressors that can be used to prevent or mitigate the impacts of anthropogenic disturbance (Berger-Tal et al., 2011). A number of behavioral variables have been used as indices of disturbance/stress (both natural and anthropogenic) in delphinid species, although reactions vary by species and stimuli, some of which have been incorporated into the Population Consequences of Disturbance Model for cetaceans (PCAD; National Research Council [NRC], 2005). For example, dusky dolphins (*Lagenorhynchus obscurus*), common dolphins (*Delphinus delphis*), spinner dolphins (*Stenella longirostris*), common bottlenose dolphins, and Risso's react to tour and other boats, human swimmers, and oil spills by variably huddling; splitting up; and changing swim speed, behavior state, and travel heading (Forest, 2001; Constantine et al., 2004; Lusseau, 2004; Bejder et al., 2006; Visser et al., 2011; Lundquist et al., 2012; Piwetz et al., 2015; Piwetz, 2018).

Our study was part of a larger baseline monitoring program to describe the distribution, abundance, and behavior of marine mammals in the U.S. Navy Southern California Training Range Complex (Figure 2) used regularly for underwater MFAS and detonation training exercises (Goldbogen et al., 2013; Henderson et al., 2014; Southall et al., 2016). The specific objectives of our study were to quantify and describe spatio-temporal patterns of group orientation/heading, cohesion, and behavior states that might be useful indicators of disturbance. This information provides a baseline for identifying and differentiating behavioral changes due to natural vs anthropogenic causes such as MFAS events in the SCB. Behavioral data also contribute to a better understanding of factors influencing intra- and inter-specific differences in the ecology of cetacean species living in the same and different regions.

Methods

Study Area/Period, Aircraft, and Equipment
From 2008 to 2012, line-transect aerial surveys and focal group follows were conducted in the SCB, extending from approximately 10 km offshore to ~70 km west of San Clemente Island, and from the Mexican border north to near Los Angeles (an area of approximately 15,500 km²) (Figure 2). This region is characterized by the Santa Catalina Island and Basin; the San Nicolas Basin; the San Clemente Island and Basin; and over eight other smaller underwater basins, seamounts, and canyons. The 15 surveys occurred at least once during 11 of the 12 calendar months: October and November 2008; June, July, and November 2009; May, July/August, and September 2010; February, March, April, and May 2011; and January, February, and March/April 2012 (Figure 2). Daily field observations typically occurred between 0900 and 1500 h Pacific Standard Time to maximize overhead light and sighting conditions. Focal group follows occurred from a twin-engine Partenavia P68-C or P68-OBS (glass-nosed) airplane equipped with bubble windows on the left and ride sides and a small porthole allowing photography and video recording.
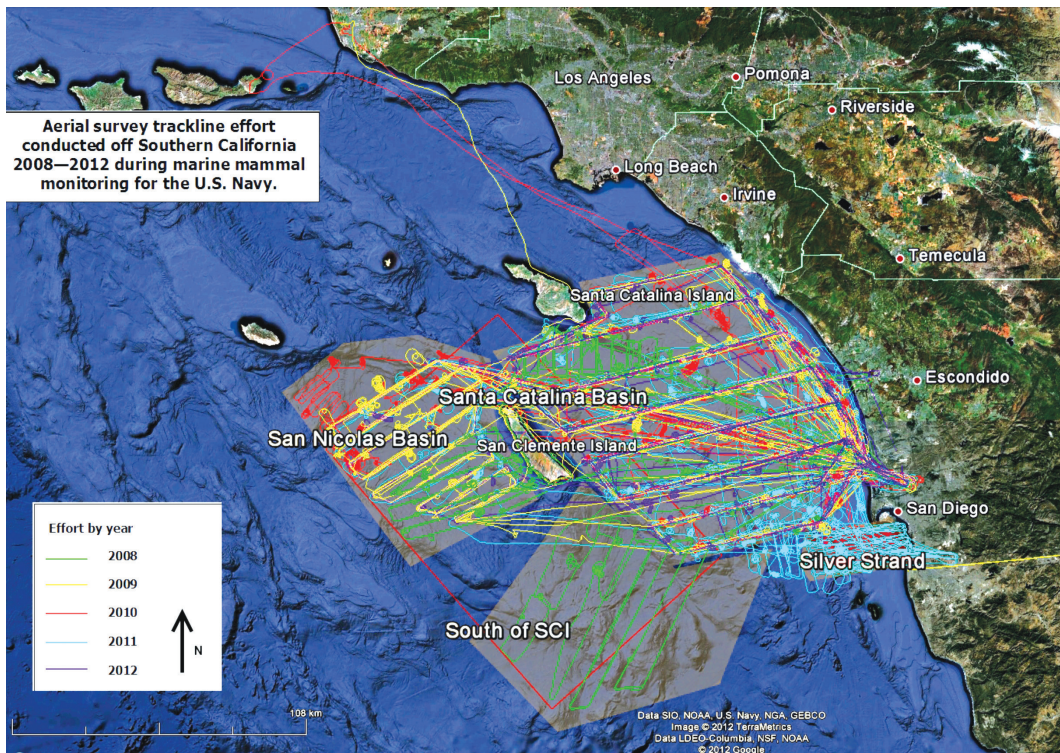
Figure 2. Survey area (delineated by gray shading) and all aerial survey effort tracklines conducted within the Southern California Bight (SCB) during the 2008 to 2012 survey period. Different colored lines indicate different survey years.

Each survey followed systematic transect lines to collect data for estimating density and abundance (for further details, see Jefferson et al., 2014b). When a Risso's group was observed under conditions suitable for a focal follow (e.g., Beaufort sea state < 4, minimal glare), aircraft altitude was increased from 335 to ~410 m and a radial distance of ~0.5 to 1.0 km outside the estimated sound cone of the aircraft to minimize potential disturbance (Richardson et al., 1995; Patenaude et al., 2002; Smultea & Lomac-MacNair, 2016). The plane then began circling the focal group to obtain detailed behavioral information. No more than two focal follows were typically conducted per day to also facilitate collection of density and abundance data according to a distance-sampling protocol (Buckland et al., 2015).

Digital imaging and software improved over the 4-year study. High-definition (HD) video was used to document behavior of focal Risso's groups using a Sony HD HDR-XR550 and HXR-NX5U NXCAM and a Canon Vixia HF10 HD digital video camera with an optical image stabilizer and 12× optical zoom video camera. Observer commentary was simultaneously recorded on the video camera's audio channel during focal follows and with a Sony digital voice recorder connected to the aircraft's audio input or with a microphone attached into an observer's headphone or a spare headphone (i.e., audio was recorded when the video was both off and on). Observers used Steiner 7 × 25 or Swarovski 10 × 32 binoculars as needed to monitor behaviors, and so on. A Suunto handheld clinometer was used to measure declination angles to groups when the sighting was perpendicular to the aircraft. GPS locations were automatically recorded at 3- to 10-s intervals on a handheld WAAS-enabled Garmin GPS and the aircraft's WAAS GPS. Data were collected by a dedicated recorder using a Palm Pilot TX (2008), Apple iTouch (2009), iPhone (2009-2010), or laptop computer (2010-2012) in a customized datasheet using *BioSpectator* (2008-2009), Microsoft *Excel* (2010-2011), or *Mysticetus* (2011-2012; www.mysticetus.com) software.

Behavioral Sampling
Instantaneous scan sampling of focal group behavior (Altmann, 1974; Mann, 1999; Martin & Bateson, 2011) using an ethogram (Table 1) was utilized to collect the following group variables once per circling of the aircraft (approximately every 60 s): (1) predominant group (≥ 50% of

Table 1. Ethogram defining Risso's dolphin (*Grampus griseus*) behavioral states based on the activity of at least 50% of the group (Smultea, 1991, 1994, 2016)

Behavioral state	Definition
Mill	≥ 50% of group swimming with no obvious consistent orientation (non-directional) characterized by asynchronous headings, circling, changes in speed, and no surface activity. Includes socializing (animals touching/within 0.5 body lengths of one another) and probable foraging involving apparent searching for/chasing of prey.[1]
Rest/slow travel	≥ 50% of group exhibiting little or no forward movement (< 1 km hr^{-1}) remaining at the surface in the same location or drifting/traveling slowly with no wake; includes rest at surface.
Medium-fast travel	≥ 50% of group swimming with an obvious consistent orientation (directional) and estimated speed ≥ 1 km hr^{-1} creating a wake or white water

[1]Heithaus & Dill (2009)

individuals) behavior state, (2) maximum nearest neighbor distance (MNND; estimated in adult body lengths [BL]; Figure 1), and (3) predominant group heading in estimated degrees magnetic relative to the plane's heading (if traveling) (per Shane, 1990; Henderson, 2010; Smultea & Lomac-MacNair, 2016). A group was defined as individuals up to 100 BLs apart within visual range of observers with > 50% of individuals engaged in the same polarized behavior state (after Norris & Schilt, 1988; Baird & Dill, 1996; Lusseau, 2004; Smultea, 2016). Within observed groups, individuals were typically within 10 to 20 BLs of each other but occasionally up to 50 to 100 adult BLs apart. A *calf* was defined as an individual less than one-half the BL of the closely accompanying larger animal and of darker gray body coloration (Hartman et al., 2016; Smultea, 2016). An observer continuously watched the dolphin group and called out behavior to a data recorder while a video operator recorded HD video through an open porthole, following general protocol developed for studying bowhead whale (*Balaena mysticetus*; Würsig et al., 1984; Richardson et al., 1985) and common bottlenose dolphin (Smultea & Würsig, 1995) behavior from a circling aircraft. A group follow occurred for 5 to 60 min (typically, 15 to 20 min), depending on environmental conditions.

Data Processing and Analyses
Data analysis involved transcribing audio recordings of behavior from video into an *Excel* spreadsheet. These data were then merged with behavioral data systematically collected in the field. In addition, digital voice recordings were used to fill in data gaps as needed such as periods when the video was not focused on the group, or the airplane wing or glare obscured the video's view. Thus, it was important to have observations/commentary from a focal observer with a wide perspective combined with video taken by a dedicated videographer. Data entered into the above-mentioned *Excel* spreadsheet included date, time, group identification number, species, group size, number of calves, heading (in degrees magnetic), MNND (estimated from video and/or in the field based on maximum number of BL between nearest neighbors), behavior state, Beaufort sea state, declination angle to sighting (to estimate distance to the focal group), the presence of any vessels or other potential disturbance (e.g., helicopters) within approximately 1 km, and comments/notes. During video/audio transcription, heading, MNND, and behavior state were noted for every 30-s period that Risso's were in view based on the most recent data collected within each 30-s period prior, starting on the minute (e.g., for the period 13:00:00 to 13:00:30 h, then 13:00:30 to 13:01:00 h, etc.).

Focal-follow data selected for analyses consisted of sequential observations on groups of Risso's. Three separate response variable rates were analyzed using collected data described as follows:

1. The *reorientation rate* was defined as change in heading (degrees) per minute (per Bowles et al., 1994; Smultea & Würsig, 1995; Gailey et al., 2007; Table 1). Observations for each focal follow were sorted by observation time. Observation times were converted to "scan times" by rounding to the next 30-s interval (e.g., observation times of 11:15:11 and 11:15:41 h were assigned scan times of 11:15:30 and 11:16:00 h, respectively). Standard multiple-linear-regression models were used to examine the relationship between heading and candidate explanatory variables. A stepwise procedure based on Akaike Information Criterion (AIC) was used to evaluate candidate models and automatically select the model with the lowest AIC (Burnham & Anderson, 2002). To avoid problems from strong associations among

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explanatory variables, initial tests of collinearity and multi-collinearity among explanatory variables were run (Belsley, 2004), and several alternate stepwise runs were conducted with different initial sets of variables.

2. The *splitting-joining* rate was defined based on observed variability in MNND, in particular, the standard deviation (SD) of this parameter (after examining the distribution of the associated raw data for patterns). Multiple linear regression was conducted (as for reorientation rate), with log-transformed SD as the response. In addition, SD of MNND was transformed into a binomial response variable (low and high SD) and was analyzed using logistic regression. Candidate explanatory variables were re-examined for evidence of association since the analysis dataset was not identical to the reorientation rate dataset. Models were selected via a stepwise AIC-based procedure as described above for reorientation rate.

3. The *behavior state transition rate* examined the rate of transitions between behavior categories among successive observations. Behavior states were categorized as rest/slow travel, mf travel, or mill. Multinomial logistic regression was used to examine the functional dependence of transitions between categories on covariate explanatory variables. Sequential analysis was conducted to assess the likelihood of a behavior state changing (i.e., a transition) during a focal group follow. Transitions between behavior states in each successive pair of observations were identified for each focal follow. A given observation at time t-1 would have behavior categorized as "mf travel," "mill," or "rest/slow travel." The subsequent observation at time t would have behavior in any one of the same three categories. Thus, there were nine possible behavior transitions: (1) mf – mf, (2) mf – mill, (3) mf – rest/slow travel, (4) mill – mf, (5) mill – mill, (6) mill – rest/slow travel, (7) rest/slow travel – mf, (8) rest/slow travel – mill, and (9) rest/slow travel – rest/slow travel. If there were n observations for a focal follow session, then there were $n – 1$ transitions for that session.

Seven explanatory variables were analyzed to assess the potential influence on the response variables reorientation rate and splitting-joining rate (Table 2), and five explanatory variables were analyzed relative to the response variable behavior state transition rate (Table 3). Two different time explanatory variables were evaluated consisting of time of day as a continuous variable based on minutes since sunrise and categorical time of day ("am" [0800 to 1200 h], "early pm" [1201 to 1600 h], and "late pm" [1601 h to dusk]), the latter with two indicator variables—*timecat1* and *timecat2*—to represent time, with "late pm" serving as the reference category.

Table 2. Response and explanatory variables used in Risso's group focal-follow analyses of reorientation rate and splitting/joining

Variable name	Type of variable	Description
Response variables		
MNND	Continuous	Maximum distance between nearest neighbors within a focal group, estimated in adult body lengths
Hdg	Ordinal	Predominant (> 50% of individuals) heading (in degrees magnetic) while traveling
Explanatory variables		
Calf	Binomial	Absent or present (0, 1)
Othergrp	Binomial	Other species absent or present (0, 1)
Boat	Binomial	Nearby boat(s) (< 1 km) absent or present (0, 1)
Season	Binomial	Cold-water (November-April) or warm-water (May-October) season (cold, warm) = (0, 1)
Month	Categorical	Categorical month (1 = November-January, 2 = February, 3 = March, 4 = April, 5 = May, and 6 = June-October)
Timecat	Categorical	Categorical time of day ("am" [0800 to 1200 h], "early pm" [1201 to 1600 h], and "late pm" [1601 h to dusk])
Tfsun	Continuous	Time (min) since sunrise; fraction of a day

Table 3. Explanatory variables used in sequential behavior state analyses based on the response variable behavior state transition rate

Variable name	Description
Calf	Calf absent or present (0, 1)
Othergrp	Other species absent or present (0, 1)
Boat	Boat absent or present within 1 km (0, 1)
Season	Cold water or warm water (cold, warm) = (0, 1)
Timecat	Time category: "am," "early pm," and "late pm"
Year	Year, categorical (2008 . . . 2012)

Based on results of the regression modeling and AIC values, the "importance value" (Burnham & Anderson, 2002) for each explanatory variable was calculated for the three analyses described above. The *importance value* was defined as the sum of the Akaike weights for each model in which that variable appeared. Thus, the importance value could range from 0 (i.e., the variable did not appear in any model) to 1 (i.e., the variable appeared in all ten models). In brief, these values represent the relative importance of each explanatory variable in explaining the response given both the set of candidate variables and the models considered.

Results

There were 51 Risso's groups recorded during focal-follow sessions ranging in duration from 5 to 59 min (mean 21.6; SD = 12.9). The number of 30-s scan periods with usable data was 1,446 for reorientation rate, 1,275 for MNND (used to calculate splitting-joining rate), and 1,359 for behavior state transition rate.

Reorientation Rate
Three stepwise runs were conducted with the following sets of candidate variables: (1) *calf*, *boat*, *othergrp*, *season*, and *timecat*; (2) *calf*, *boat*, *othergrp*, *month*, and *tfsun*; and (3) *calf*, *boat*, *othergrp*, *month*, and *timecat*. All three stepwise runs resulted in selection of the same model in which the only covariate was *othergrp*. The fitted model was reorientation rate = 10.822 + 5.5201 × *othergrp*. Thus, the only explanatory variable that appeared to influence reorientation rate was the presence of other marine mammal species with the Risso's group, such that the mean reorientation rate when other species were present was greater by 5.52 degrees/min than when other species were absent (Figure 3). However, the 90% confidence interval for this difference spanned zero (-1.51, 12.55), indicating that the difference was not statistically significant.

Splitting-Joining Rate
None of the explanatory variables were found to influence splitting-joining rate of focal Risso's groups and thus did not improve model fit.

Behavior State Transition Rate
Overall, focal groups spent most of their time engaged in rest/slow travel (60% of 1,359 records), followed by mf travel (33%). Mill behavior was rare (7%). Risso's rarely changed behavior state during focal follows (Table 4). Results showed that any behavior observed at time *t*-1 was most likely to be followed by the same behavior at time *t*. Although all possible transitions did occur, they were infrequent. Time of day and calf presence contributed to the most variability in the regression model with the highest importance values (Tables 5 & 6).
    Calf Presence—When calves were present, Risso's were 4.28 times more likely to continue mf travel than were groups with no calves (based on odds ratio results from estimated regression coefficients; Table 7). Similarly, groups with a calf were more likely to transition from mf travel to mill and from mill to mf travel than non-calf groups (relative to slow-slow transitions).
    Time of Day—mf-mf transitions were less likely during mornings than later in the day. Conversely, Risso's groups were six times more likely to continue mf travel in the early afternoon than in the early morning and late afternoon. The probability of transitioning from slow to mf travel increased for Risso's groups across the day.

Discussion

Interpretation of results in the context of other studies are described below for the examined response variables of reorientation, splitting-joining, and behavior state transition rates among Risso's. The biological meaning of relationships to explanatory variables contributing most prominently to influencing response variables are also examined and consisted of calf presence and time of day factors.
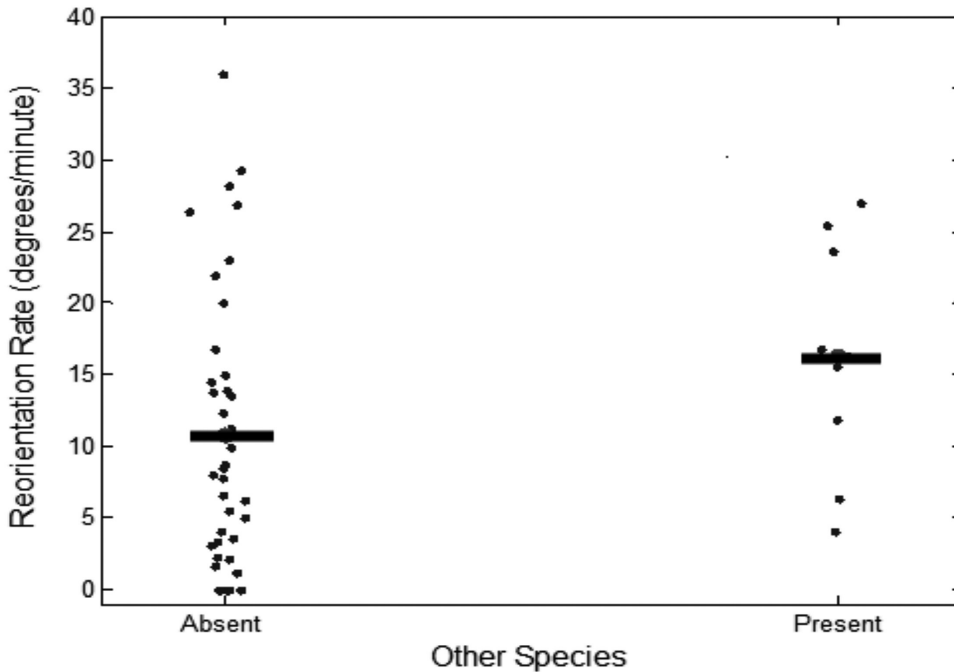
Figure 3. Mean reorientation rate as a function of presence/absence of other species within dolphin groups: observed reorientation rate for 47 focal-follow sessions (small circles); rate predicted by linear regression model (horizontal bars). Circles have been jittered along the horizontal axis for greater clarity.

Table 4. Counts of behavior state transitions

		Time t-1		
		Medium-fast travel	Mill	Rest/slow travel
Time t	Medium-fast travel	405	12	29
	Mill	15	55	20
	Rest/Slow travel	21	19	783

Reorientation Rate

Risso's groups exhibited a higher reorientation rate in the presence of other marine mammal species (*othergrp*), suggesting that Risso's change headings more often when intermixed with other species. Although hampered by small sample size, this may be biologically meaningful and related to a tendency to socially interact with (i.e., orient toward) other species and/or, conversely, to move away from them based on previous studies. Inter-specific associations are often associated with prey aggregations (Shane et al., 1986; Acevedo-Gutiérrez, 1991; Vaughn et al., 2007) within which species may compete for food or space. Our pre-liminary interpretation of videos of Risso's with

common bottlenose dolphins suggests that the bottlenose dolphins were following the Risso's and were also seen swimming between individual Risso's; thus, the bottlenose dolphins appeared to be "separating" the Risso's. This may be a form of aggression or inter-specific competition as has been suggested previously for these two species in the SCB (Shane, 1995b). A larger sample size and future studies are needed to further investigate this inter-specific behavior.

Splitting-Joining Rate

Identification and analysis of the splitting-joining rate response variable was an attempt to determine if differences in MNND could be attributed to any

Table 5. Top ten multinomial logistic regression models for Risso's behavior state transition rate; Δ_i is the difference AIC_i to AIC_1, and w_i is the Akaike weight.

Model rank	Model	AIC_c	Δ_i	w_i
1	*Calf, timecat1, timecat2*	1,643.6	0.0	0.9997
2	*Timecat1, timecat2*	1,659.9	16.3	0.0003
3	*Season, timecat1, timecat2*	1,720.5	76.9	0
4	*Mixedgrp, timecat1, timecat2*	1,742.8	99.2	0
5	*Calf*	1,774.6	131.0	0
6	*Calf, boat*	1,783.6	140.0	0
7	*Calf, season*	1,784.5	140.9	0
8	*Season*	1,791.2	147.6	0
9	*Boat*	1,797.9	154.3	0
10	*Boat, season*	1,806.4	162.8	0

Table 6. Importance values for all explanatory variables in the top ten models for Risso's behavior state transition rate based on sequential behavior analysis

Variable	Importance
Timecat1, timecat2	1.00
Calf	0.97
Season	0.00
Mixedgrp	0.00
Boat	0.00

of the explanatory variables examined. However, given the high variation in the splitting-joining rates as defined herein, no significant relationships were evident.

Behavior State Transition Rate
The overall predominance (60%) of slow behavior (i.e., rest/slow travel) observed among focal Risso's during our daytime observations is characteristic of other delphinid species that feed at night and rest during the day. For example, Hawaiian spinner dolphins and dusky dolphins off Kaikoura, New Zealand, predominantly rest and socialize during daytime near shore, gradually increasing their surface activity, socializing, and group sizes across the afternoon before moving offshore to actively feed at night in large aggregations when squid and mesopelagic fish prey move closer to the water surface with the deep scattering layer (Norris & Dohl, 1980; Würsig & Würsig, 2010). Shore-based focal follows of Risso's groups in the Azore Islands similarly found that Risso's predominantly rested during daylight (Visser et al., 2011).

Very little is known about nighttime behavior of Risso's. The handful of stomach contents analysis studies from around the world (reviewed in Bearzi et al., 2010) combined with Risso's reduced dentition suggest that they subsist primarily on mesopelagic squid and fish that inhabit deep waters and rise at night with the DSL (Clarke, 1986; Cockcroft et al., 1993; Baird, 2009; Bearzi et al., 2010; Jefferson et al., 2015). It is, therefore, generally thought that Risso's forage mainly at night (Shane, 1995a, 1995b; Praca & Gannier, 2007; Soldevilla et al., 2010, 2011). Soldevilla et al. (2010) hypothesized that Risso's in the SCB feed predominantly at night based on increased nocturnal vocalization rates. Limited results from a small number of Risso's tagged with time-depth recorders in the SCB found that deeper dives occurred near dawn and dusk as compared to daytime (G. Schorr, Marine Ecology and Telemetry Research, pers. comm., December 2017). However, in other regions, Risso's appear to feed frequently during daytime. Kruse et al. (1999) found that Risso's foraging behavior patterns in Monterey Bay varied with season, year, and location. It is likely that Risso's, like other delphinids such as dusky, Hawaiian spinner, common bottlenose, and common dolphins, adapt their temporal foraging habits to the availability and spatio-temporal distribution, abundance, and behavior of their prey. This would explain why Risso's in Monterey Bay appear to feed more during daytime than those in the SCB. We observed Risso's apparently foraging during the day on only three occasions during 2008 to 2013 (Smultea, 2016). In all cases, individuals were spread much farther apart than at any other time we observed groups of Risso's, on the order of 20 to 100+ BL apart, and they exhibited fast, steep dives characterized by bubble trails. During these three foraging occasions, individual Risso's were frequently followed by northern right whale dolphins, possibly to take advantage of Risso's foraging finds through kleptoparasitism as

Table 7. Parameter estimates and odds ratios for the top-ranked Risso's behavior state transition sequential model

Logit behavior state[1]	Parameter	Estimate	Std error	L95	U95	Odds ratio
mf – mf	*Intercept*	-2.1670	0.2813	-2.7558	-1.5783	
	Calf	1.4544	0.1617	1.1159	1.7928	4.28
	Timecat1	-0.6957	0.3191	-1.3635	-0.0278	0.50
	Timecat2	1.8022	0.2844	1.2069	2.3975	6.06
mf – mill	*Intercept*	-5.2649	1.0730	-7.5108	-3.0190	
	Calf	1.7839	0.5514	0.6298	2.9379	5.95
	Timecat1	-0.1371	1.1297	-2.5015	2.2273	0.87
	Timecat2	1.2238	1.0681	-1.0117	3.4593	3.40
mf – slow	*Intercept*	-27.8	66097.	-138370.	138315.	
	Calf	0.5972	0.5163	-0.4835	1.6779	1.82
	Timecat1	23.7	66097.	-138319.	138366.	2.03×10^{10}
	Timecat2	24.5	66097.1	-138318.	138367.	4.34×10^{10}
mill – mf	*Intercept*	-5.7907	1.1328	-8.1616	-3.4198	
	Calf	2.4950	0.6389	1.1577	3.8324	12.12
	Timecat1	-0.8800	1.2378	-3.4709	1.7108	0.41
	Timecat2	1.2736	1.0766	-0.9797	3.5269	3.57
mill – mill	*Intercept*	-3.2639	0.5248	-4.3624	-2.1654	
	Calf	0.6194	0.3026	-0.0139	1.2527	1.86
	Timecat1	0.6989	0.5447	-0.4412	1.8390	2.01
	Timecat2	0.1641	0.5693	-1.0274	1.3556	1.18
mill – slow	*Intercept*	-4.4672	1.0176	-6.5971	-2.3373	
	Calf	0.0499	0.5910	-1.1871	1.2869	1.05
	Timecat1	0.5879	1.0771	-1.6664	2.8422	1.80
	Timecat2	0.9621	1.0547	-1.2454	3.1697	2.62
slow – mf	*Intercept*	-3.5461	0.6098	-4.8224	-2.2698	
	Calf	0.6051	0.4299	-0.2947	1.5048	1.83
	Timecat1	-0.2059	0.6714	-1.6111	1.1993	0.81
	Timecat2	0.3313	0.6463	-1.0214	1.6839	1.39
slow – mill	*Intercept*	-4.4570	1.0168	-6.5852	-2.3288	
	Calf	0.0104	0.5868	-1.2178	1.2386	1.01
	Timecat1	0.5912	1.0770	-1.6630	2.8454	1.81
	Timecat2	1.0435	1.0509	-1.1560	3.2431	2.84

[1]mf = medium-fast travel

suggested by Smultea et al. (2014). These observations suggest that if prey are available, Risso's also feed during daytime in the SCB. However, the preponderance of evidence from the SCB suggests that most foraging occurs crepuscularly and/or at night, and resting is most common during daylight.

Predominant rest/slow travel by focal Risso's groups (60%) strongly contrasted SCB common dolphins, which rarely exhibited rest/slow travel based on analysis of first-observed behavior states (3% of 555 groups) by Smultea (2016). Also in contrast, common dolphins frequently milled (38%; Smultea, 2016), while our focal Risso's did not (7%). We believe this is related primarily to reported differences in predominant prey and apparent diurnal (commons) vs nocturnal (Risso's) foraging habits in the SCB (Pusineri et al., 2007; Henderson, 2010; Soldevilla et al., 2010, 2011). However, the 60% for rest/slow travel among Risso's focals is nearly twice as frequent as indicated for first-observed behavior analyses of Risso's reported in Smultea (2016) (32% of 290 Risso's sightings were rest/slow travel). Note that only the first behavior state was

recorded for each of the latter sightings vs focal follows where behavior state was noted every 30 s for the same group. Similarly, Karniski et al. (2015) found that differences in data collection protocol for common bottlenose dolphins (e.g., duration spent observing) resulted in differences in ethogram activity budgets.

Risso's rarely changed behavior state during focal follows. Results clearly showed that any particular behavior observed at time t-1 was most likely to be followed by the same behavior at time t. Although all possible transitions did occur, transitions from one behavior state to another were infrequent. However, the likelihood of transitioning from slow to mf travel increased across the day for Risso's groups. This is again similar to diurnal behavioral patterns reported for nocturnal-feeding Hawaiian spinner and Kaikoura dusky dolphins (Norris & Dohl, 1980; Würsig & Würsig, 2010, respectively).

Calf Presence—When calves were present, Risso's were 4.28 times more likely to continue mf travel than were groups with no calves (based on odds ratio results from estimated regression coefficients). The reason for this pattern is unknown but may be related to predation pressure, location, or other parameters. More detailed analyses focused on groups containing a calf in the SCB may reveal reasons for our observed differences related to calf presence. In the Azores, Hartman et al. (2014) found that Risso's mother–calf pairs exhibited different habitat selection, social, and behavior patterns than other age/sex classes. Mother–calf groups preferred shallower nearshore waters and were segregated from other age and sex classes inhabiting more offshore deep waters. Smultea (2016) found that Risso's groups with calves were significantly larger, and MNND were significantly closer with calf presence. Identifying specific habitat needs of mothers and calves is important for conservation and management of this species given that calf survival is integral to sustained populations. Similarly, focal Risso's groups with calf presence were more likely to transition from mf travel to mill and from mill to mf travel than non-calf groups (relative to slow-slow transitions). This suggests that socializing and possibly foraging may occur more frequently among groups with a calf (by definition, *mill* is associated with animals orienting toward one another, touching, and/or participating in sudden, apparent foraging sprints). Detailed video analyses focusing on this behavior would help explain this pattern.

Time of Day—During mornings, mf to mf travel transitions were less likely than later in the day. In the early afternoon, Risso's groups were six times more likely to continue mf travel as compared

to early morning and late afternoon. This suggests that during afternoon traveling, Risso's tend to keep traveling. We hypothesize that as dusk approaches, they are transiting to nocturnal foraging areas, transitioning from earlier social and rest activity. Similarly, spinner dolphins (Norris & Dohl, 1980) and dusky dolphins (Würsig & Würsig, 1980, 2010) rest and socialize during the morning, with their activity level increasing in the afternoon before moving offshore to feed in deeper waters.

Conclusions

In summary, the behavior state of Risso's was significantly related to calf presence and time of day. Their predominant rest/slow travel behavior during daytime contrasts that of the other most common delphinid in the SCB, the common dolphin (Smultea et al., 2014; Smultea, 2016). This difference is likely related to the presumed nocturnal foraging habits of Risso's. Risso's are considered a good candidate focal species to study regarding the potential effects of the relatively high level of Navy MFAS training activities that occur in the SCB. This is based on (1) their common occurrence in relatively high numbers (Forney & Barlow, 1998; Carretta et al., 2000; Smultea et al., 2014; Jefferson et al., 2014a); (2) their tendency to remain at or near the surface for extended periods compared to other species, thereby allowing longer observation periods (Smultea, 2016); (3) their light body coloration facilitating tracking, including below the water surface to depths of approximately 10 to over 15 m (Smultea, 2016); (4) their identification as a priority species in the U.S. Navy's Southern California Monitoring Plan and the Southern California Behavioral Response Study (BRS) (e.g., Southall et al., 2012); and (5) a significant tendency to rest/slow travel—for example, if Risso's were to react to MFAS, a change in behavior state from the predominant rest/slow travel and movement away from the disturbance might be expected. This behavior state transition has frequently been reported among other delphinids as a significant change in response to anthropogenic disturbance, including to vessels and tour boats (Constantine et al., 2003, 2004; Lusseau, 2003, 2004; Bejder et al., 2006; Lundquist et al., 2012; Piwetz et al., 2015; Piwetz, 2018) and human swimmers (Orams, 1997; Constantine, 2001; Forest, 2001). A more detailed examination of video and field data, including other response (e.g., dive and surface duration) and explanatory variables, may reveal other significant baseline patterns that may be sensitive indices of disturbance.

It is important to note that cetaceans are hardly ever individuals but are, instead, socially complex

groups of animals. It is critically necessary that an evaluation of disturbance includes evaluation of group behaviors, social interactions, distances apart, potential changes or masking of vocalizations, and—as possible—assessments of changes in affiliations. Changes in overall group behavioral patterns and social disruption are likely to be important as responses to anthropogenic activities. These factors must be considered when evaluating potential effects (or lack thereof) of U.S. Navy activities on marine mammal species, particularly differences east and west of San Clemente Island given the expected higher level of U.S. Navy MFAS training activities west of this island.

Acknowledgments

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