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Synchrony, leadership, and association in male Indo-pacific bottlenose dolphins (*Tursiops aduncus*)

running title: Synchrony and behavior in dolphins

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Abstract

Male Indo-pacific bottlenose dolphins in in Shark Bay, Western Australia, have converged with humans in the formation of nested male alliances and the use of synchrony in alliance behavior. Further, the strength of association among allied male dolphins varies and the stability of alliances correlates with the rate that males consort with estrus females (and is thus a possible indicator of dominance). To examine the possibility that synchrony reflects alliance association strength and dominance relationships, we analyzed videotapes from focal follows of two groups of males that reflect the range of alliance size and the strength of association between individuals in the population. We examined two variables; *leadership* during synchronous behaviors, based on which animal in a synchronously surfacing pair surfaced first, and the *degree of synchrony*, based on temporal differences in synchronous surfacing. We predicted that closer associates would exhibit a greater degree of synchrony and that one dolphin in a dyad would consistently lead. Contrary to our predictions, the degree of synchrony was inversely related to strength of association within alliances. This surprising result suggests that individuals with less secure bonds may strive more to achieve synchrony. We found no evidence of leadership during synchronous surfacing or between synchrony and other behavioral variables. Proximate mechanisms for synchronous behavior, such as entrainment and mutual motor imitation ('the mirror game' paradigm), may inhibit leadership in this context. Our results show that synchrony during surfacing is not a useful behavior to examine for dominance relationships in wild dolphins but it may be a useful tool to examine variation in alliance relationships.

Keywords: alliances, coalitions, cooperation, entrainment, joint imitation, mirror game paradigm

Introduction

Synchrony is a term that has been used to describe behaviors that are merely clustered in time or overlapping in occurrence as well as those that occur in unison (see Duranton & Gaunet, 2016; Ravignani, 2017). Here we are interested in behaviors that occur in unison or, as defined by Ravignani (2017), that exhibit a 'precise coincidence of events in time.' Such synchrony has been reported in a variety of animals, for instance, in mating contexts such as the courting displays by western grebes (Nuechterlein & Storer, 1982) and mate attraction by fiddler crabs waving their major claws (Backwell et al., 1999; Backwell, 2019). Spectacular synchrony is found in the flashing of some fireflies (Buck, 1938; 1988); males of one species signal females by producing flashes that occur within 16 milliseconds of each other during a 560 millisecond flash cycle (Buck & Buck 1968). Other striking examples of synchrony have evolved under the threat of predation, as in the responses to disturbance by schooling fish and flocking starlings (e.g. Pitcher & Parrish, 1993; Larsson, 2012; Cavagna et al., 2010).

Evidence of movement synchrony in non-human primates is scarce. Macaques spontaneously synchronize their movements while performing some tasks in tandem (Nagasaka et al., 2013). In humans, movement (or motor) synchrony is found in a range of contexts, including walking, rocking in chairs, marching, music, and dance (Hagen & Bryant, 2003; McNeill, 1995; Richardson et al., 2007; Zivotofsky & Hausdorff, 2007; van Ulzen et al., 2008; Miyake, 2009; Repp & Su, 2013) and has been linked to social relationships and interactions, including cooperation, prosocial behavior, and mother-infant interactions (McNeill, 1995; Wiltermuth & Heath, 2009; Valdesolo et al., 2010; Trainor & Cirelli, 2015; Cirelli et al., 2017; Cirelli, 2018), as well as increasing feelings of similarity, compassion, sympathy, and altruism between human partners (Valdesolo & DeSteno, 2011).

Synchrony is frequently observed in odontocetes. Synchronous breathing occurs during resting bouts in killer whales (*Orcinus orca*) and spinner dolphins (*Stenella longirostris)* (Norris & Dohl, 1980); and in response to boat traffic in Guiana dolphins (*Sotalia guianensis*) and bottlenose dolphins (*Tursiops sp.)* (Tosi & Ferreira, 2009; Miller et al., 2008; Hastie et al., 2003; Constantine et al., 2004). Captive bottlenose dolphins (*Tursiops sp*.) engage in synchronous swimming after the introduction of unfamiliar objects into their habitat (McBride & Hebb, 1948). Newborn bottlenose dolphin calves surface synchronously with their mothers after birth, but the rate of synchrony declines sharply in the first few weeks (Mann & Smuts, 1999; Fellner et al., 2006). Synchronous surfacing in pilot whales (*Globicephala melas*) may function generally in the maintenance of social bonds and as a response to disturbance (Senigaglia & Whitehead, 2012; Senigaglia et al., 2012). In Mikura Island, Japan, synchronous female pairs of Indo-pacific bottlenose dolphins (*Tursiops aduncus*) swim closer together than synchronous male pairs (Sakai et al., 2010).

In Shark Bay, Western Australia, Indo-Pacific bottlenose dolphins have converged to a striking degree with humans in nested male alliance formation and synchrony (Connor, 2007). The male dolphins form three levels of nested alliances; males cooperate in pairs and trios (1st-order alliances) to form consortships with individual females, teams of 4-14 males (2nd-order alliances) cooperate against other groups in contests over females, as do pairs of 2nd-order alliances (3rd-order alliances) (Connor et al., 1992a; b; Connor, 2007; Connor et al., 2011; Connor & Krützen, 2015). Males nearly always recruit 1st-order allies from within their 2nd-order alliance, which may persist for decades and is considered the core social unit of males in Shark Bay (Connor & Krützen, 2015). Association in 2nd-order alliances is based on association history and age similarity rather than kinship (Gerber et al., 2019).

First-order alliances vary in association strength and stability; some strongly associating male pairs and trios are almost always found together and their association may persist for more than two decades; while other males change 1st-order allies to varying degrees between consortships (Smolker et al., 1992; Connor et al., 1992a; Connor et al., 2001; Connor & Krützen, 2015). The stability of 1st-order alliances varies within 2nd-order alliances and is correlated with the rate males consort estrus females, suggesting dominance relationships, which have been described in one captive study only (Samuels & Gifford, 1997). Association strength also varies within stable 1st-order trios (Smolker et al., 1992).

Synchrony is a striking feature of male alliance behavior and may be used to advertise alliance relationships, increase the perceived formidability of allies, and help establish and maintain social bonds (Connor et al., 2006; Connor, 2007; Fessler & Holbrook, 2016). In dolphin synchronous surfacing, two males, but sometimes more, will surface to breathe side-by-side (< 2 meters apart) synchronously (Connor et al., 2006). Such synchrony is found in a range of behavioral contexts including traveling, resting, and socializing. Connor et al. (2006) examined synchronous surfacing between males that associated in small 2nd-order alliances (4-6 males) composed of stable 1st-order alliances. They found that synchrony reflected association strength and behavioral context; when all three males in a stable trio were together, the top two associates surfaced synchronously more often than either did with the third male. When two 1st-order alliances were together, males more often surfaced synchronously with members of their 1st-order alliance. However, two males from different 1st-order alliances were more likely to surface side-by-side synchronously during excited social behavior around a consorted female, suggesting a tension-reduction function (Connor et al., 2006).

Male dolphins also perform synchronous displays around females (see SI). These displays, which often involve synchronous underwater turns and aerial leaps, sometimes in opposite directions, may serve to impress consorted females (see Connor et al., 2000; Connor et al., 2006). Typical side-by-side synchronous surfacing may be a component of a more elaborate display. For example, a display may include males swimming alongside a female, turning out synchronously in front of her, swimming back past her, turning in and surfacing side-by-side behind her (Connor et al., 2006).

The synchronous surfacing (synchs) between dolphins in Shark Bay were revealed to be slightly asynchronous in frame-by-frame video analysis (Connor et al., 2006; the heads of synchronously surfacing males emerged 7-9 frames apart on average, which corresponded to 120-150 milliseconds filming at 60 frames/sec; see SI). These slight time delays presented an opportunity to examine synchrony for evidence of leadership, and an effect of association strength and behavioral context on the degree of synchrony.

In other mammals, leadership is commonly examined in the context of collective decisions such as group movement. For example, older females, who may be valuable allies and have more ecological knowledge than their younger counterparts, lead group movements in bonobos and killer whales (Brent et al., 2015; Tokuyama & Furuichi, 2017) and determine the group response to a potential threat in elephants (McComb et al., 2011). Leadership during group movements has been reported in common bottlenose dolphins (*T. truncatus*) in Florida, based on the proportion of direction changes initiated by individuals (Lewis et al., 2011).

Based on the report of leadership in bottlenose dolphin group movements and the differences in surfacing we detected in frame-by-frame analysis, we posited that leadership might be present in synchronous surfacing as well. Patterns of leadership during synchronous behavior might reflect important parameters of male-male relationships, such as dominance (see Samuels & Gifford, 1997) and hence predict paternity success.

The dolphin alliance relationships are based on cooperation to improve access to estrus females (Connor, 2010). Further, the synchrony in dolphins, bird flocks, and fish schools is likely based on a simple form of cooperation, by-product mutualism (Connor, 1995). Studies on diverse taxa, including primates, carnivores, and birds, show that individuals prefer to cooperate or cooperate better with partners with whom they share stronger bonds (e.g. Asakawa-Haas et al., 2016; Marshall-Pescini et al., 2017; Molesti & Majolo, 2016; Schwing et al., 2016). We therefore predicted, following our previous finding that closer associates engage in synchrony more often (Connor et al. 2006), that dolphins with stronger associations would also be more synchronous.

Finally, given that the occurrence of synchs between members of different 1st-order alliances varied with behavioral context (Connor et al., 2006), it seemed possible that the precision of synchronous surfacing might vary with behavioral context (e.g. resting vs. socializing, presence or absence of consorted females).

We asked: 1) if there were consistencies in *leadership* in synchs, for all individuals and with respect to alliance membership and level of association in dyads, 2) if there were differences in the *degree of synchrony* among pairs related to the strength of association, and 3) if there were differences in the degree of synchrony related to behavioral context, including the presence of consorted females. Finally, 4) we tested for an effect of differences in consortship rate between individuals in a dyad on leadership and degree of synchrony.

Methods

We used data from a video-based study (1994-1997) on the behavior and vocalizations of a large 14-member 2nd-order alliance (WC group, Connor et al., 1999; 2001) and a small 5-member 2nd-order alliance (RH group) that included males from the previous synchrony study (Connor et al., 2006). WC group males formed much more labile 1st-order alliances than males in the RH group (Connor et al., 1999; 2001). Given that the RH and WC groups are at opposite extremes of a continuum of group size and 1st-order alliance stability (Connor et al., 2011; Connor & Krützen, 2015), our study should detect any patterns of synchrony that exist among males in the Shark Bay population.

All observations were made from two small powerboats (3.5 and 4.5 meters). Encountered dolphin groups were surveyed for at least five minutes for group composition, location, predominate group activity, and environmental variables. Individuals were identified by their distinct dorsal fin shapes and scars, and group membership was based on the 10-meter chain rule (Smolker et al., 1992).

We determined the strength of association between males using the half-weight index (HWI), derived from survey sightings of dolphins in traveling, resting, and socializing groups (following Connor et al., 2001). The HWI formula (Cairns & Schwager, 1987) is:

$$\mathrm{HWI} = \frac{x}{x + y_{ab} + \frac{1}{2}(y_a + y_b)}$$

where x is the number of times individual *a* and individual *b* are seen associated, y_{ab} is the number of times individual *a* and individual *b* are seen separately in the same sampling period, y_a is the number of times individual *a* is seen without individual *b*, and y_b is the number of times individual *b* is seen without individual *a*.

During focal follows on individual males (1-8 hours), we recorded behavior and associations, as well as dolphin vocalizations captured by a hydrophone, on a Panasonic model AG-3P S-VHS camera fed to a JVC BR-S405U portable video deck (see also Vollmer et al., 2015). One observer dictated behaviors while an assistant video-taped the dolphins. Occasional discrepancies occurred when the observer was not looking in the area that the camera was filming, resulting in three categories of observed synchs: 1) those only called out by the observer (not included in this analysis), 2) those called out by the observer and captured on video, and 3) those only captured on video.

We conducted frame by frame video analysis of synchronous surfacing recorded during 62 focal follows on members of the large 2nd-order alliance, WC group (163 hours), and 38 focal follows on members of the small 2nd-order alliance, RH group (82 hours) using a Panasonic AG 7350 VCR. Following Connor et al. (2006), we analyzed only synchs of dyads that were no more than one body length apart and a half-body length in stagger. The leader was scored as the dolphin whose head emerged from the water first, and the degree of synchrony was determined by the number of frames (at 60 frames/second) that occurred between the emergence of the head of the first and second animal. Other variables recorded with each synchronous surfacing included group membership, the presence of consorted females, and behavioral context.

The behavioral context of a synch was defined based on behaviors that occurred within two minutes of each synch (following Connor et al., 2006). If a synch occurred and no social behaviors were observed that synch was identified as 'non-social;' if petting (contact between the pectoral fin of one dolphin and any part of another dolphin (Connor et al., 2000)) was observed that synch was identified as 'social,' and if any other social behaviors beyond petting were observed that synch was identified as 'intense social.' Intense social behaviors include leaps, chases, and sexual behaviors (Connor et al., 2006). If a synch was called and no surface activity was observed but popping vocalizations were heard that synch was identified in the 'pops' category. Pops are a threat vocalization employed by males consorting females (Connor et al., 2006; Vollmer et al., 2015; King et al., 2019). We further identified synchs between males that were in the same (=intra-alliance) or different 1st-order alliances (=inter-alliance) and whether a female was in a consortship with one, both, neither of the males, or with other males in the group.

We calculated a consortship rate for each male as the ratio of the number of days a male was observed in a consortship, divided by the total number of days the male was observed (Connor et al., 2001; 2017). We compared synch dyads in the WC group that had contrasting consortship rates for leadership and degree of synchrony (see SI for details).

To assess whether some individuals were consistent leaders we calculated the proportion of times that each individual was a leader in all of their dyadic synchs. Uncertainty intervals were estimated using a simulated Bernoulli process (n = 10,000) with a probability of 0.50 for each individual where the number of trials was equal to the number of observed synchs for those animals. A success (1) represented leading in a synch and failure (0) represented following. Intervals were calculated from the 0.025 and 0.975 quantiles of successes divided by number of trials and compared to the observed values.

To test if closer associates were more egalitarian in leadership we calculated a leadership share index as the deviation from a 50/50 split of leadership in each dyad. Leadership share ranges from 0 to 1, with 0 indicating leadership during synchs is split exactly 50/50 and 1 indicating that one animal always leads and the other always follows. This leadership share was used as the response variable in a linear mixed model estimated using the R package 'lme4' (R Core Team, 2019; Bates et al., 2015). HWI was considered as a fixed effect to represent level of association. To test if level of association predicts degree of synchrony we used a similar model with mean number of video frames apart as the response variable and HWI as a fixed effect.

To distinguish between inter- and intra-alliance synchs in the presence of consorted females, we determined 6 categories: intra-alliance synch with no consorted female present (NF);

intra-alliance synch between males with a consorted female (WF); intra-alliance synch between males, but the female consorted by other males in the 2nd-order alliance (WNF); inter-alliance synch between 2 males with a consorted female present with one of the two males in the synch (A1F) ; inter-alliance synch between 2 males, and each male has a consorted female (A2F); and inter-alliance synch between 2 males that do not have a consorted female but a consorted female is present (consorted by a different alliance; AFO).

Finally, to determine if behavioral context predicts degree of synchrony, we constructed a model with number of frames as the response variable and behavioral context and the presence of consorted females within (intra-) and among (inter-) alliances as categorical predictor variables. In this model each observation was a single synch in contrast to the previous models where each observation was a single dyad.

All three linear mixed models included a fixed effect for 2nd-order alliance membership, and two random intercepts for each individual ID in the dyad. Only dyads with at least five observed synchs were included in the models. We assessed significance of fixed effect coefficients if the 95% confidence intervals did not cross zero.

Ethical statement: data were collected under permits from the Western Australian Department of Parks and Wildlife and followed the ABS guidelines for the treatment of animals in behavioral research and teaching.

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Results

From 163 hours of video footage, we obtained 579 pairwise synchs over 41 observation days between members of the 14-member 2nd-order alliance, the WC group, and 82 video hours yielded 193 pairwise synchs over 21 observation days between males in the 5-member 2nd-order alliance, the RH group. The 19 individual males were recorded in 43-136 synchs (mean = 81.3, sd = 30.0) on 7-23 days (mean = 16.7, sd = 4.4) and the maximum percentage of a male's synchs that occurred on one day ranged from 8.1 to 43.1(mean = 21.6, sd = 8.4).

Leadership

We calculated the proportion of times that each individual was a leader in all of their dyadic synchs. All observed proportions of leadership were within the 95% uncertainty intervals calculated by simulation (Figure 1).

We also investigated leadership among specific dyads (Figure 1) and tested if 2nd-order alliance membership and level of association (HWI) predicted leadership share for each dyad in a linear mixed model (26 dyads; 19 individuals; 438 total synchs). HWI was not a significant predictor of leadership share in the model and there was no significant difference between the 2nd-order alliances (Table 1). Differences in consortship rate within dyads were not a predictor of leadership share (see SI).

Degree of Synchrony: association level

We tested if level of association (HWI) was a predictor for degree of synchrony using a linear mixed model (26 dyads; 19 individuals; 438 total synchs). HWI was a significant positive predictor of number of frames (Table 2) indicating that closer associations were less synchronous (Figure 2; see SI).

Degree of Synchrony: behavioral context

Dyads in the large WC and small RH 2nd-order alliances were examined for their degree of synchrony during each behavioral context (n = 440 synchs), including the presence of consorted females. In a linear mixed model neither behavioral state nor presence of consorted females were significant predicators of degree of synchrony (Table 3; see SI). There was a significant difference between the two 2nd-order alliances in degree of synchrony in this model (Table 3, see SI). Differences in consortship rate within dyads were not a predictor of degree of synchrony (see SI).

Discussion

The first variable we examined was leadership. We did not find evidence for consistent synchrony ‘leaders’ among allied males in this population. While there is some variation in how often individuals are leaders versus followers in synchs, many animals led about as often as they followed. Similarly, the level of association between males (based on the half-weight index, HWI) as well as differences in consortship rate between individuals surfacing synchronously did not predict how egalitarian dyads are in trading off leadership.

A consideration of proximate mechanisms for dolphin synchrony may help us understand why we did not find evidence of leadership. In their important review, Wilson and Cook (2016) suggested that the synchrony observed in cetaceans and many other taxa may be based on entrainment. Entrainment occurs when the rhythmic output by one individual becomes the rhythmic input for another. When two individuals are the input and output for each other, mutual entrainment occurs (Miyake, 2009; Phillips-Silver et al., 2010; Repp and Su, 2013; Trost et al., 2017). For bottlenose dolphins, synchronous surfacings may be based on entrainment or mutual entrainment much like humans walking in stride with their partner (Miyake, 2009). Mutual entrainment, or entrainment by one individual in a dyad, where individuals can anticipate the tempo (e.g. Gámez et al., 2018), will not reveal leadership. Entrainment is thought to be important in vocal learners like dolphins (Janik, 2014), and uncommon elsewhere, but the review by Wilson & Cook (2016) suggests that entrainment is more widespread.

This entrainment hypothesis, however, does not extend easily to the synchronous displays that males perform around females, which often include typical side-by-side ‘synchs’ as components, as well as complex aerial and underwater leaps, turns, and other movements (Connor, 2007). These highly variable synchronous displays we observe in Shark Bay are similar to the novel (unconditioned) synchronous behaviors that trained captive dolphins generated on command (Herman, 2002). Herman (2002; 2010) invoked imitation to explain the novel synchronous behaviors as dolphins have superb abilities to imitate (copy novel behavior) in the vocal and motor domains (Herman, 2010; Richards et al., 1984). In ‘classical’ imitation, one individual performs a behavior that is then copied by another (see McEllin et al., 2018) so Herman (2002; 2010) should have been able to detect leadership in the dolphins’ novel synchronous behavior. Careful examination of video failed to reveal a leader, however, which suggested to Herman (2002; 2010) that leadership could be based on subtle body cues that indicate intent to engage in synchrony. Similarly, in Shark Bay, future studies using drones may be able to detect which dolphin approaches the other to initiate a bout of synchrony.

We suggest that synchronous dolphins may be engaged in ‘mutual’ or ‘joint’ motor imitation, rather than ‘classical’ motor imitation where one individual closely copies another (McEllin et al., 2018). In humans, Noy et al. (2011) examined the ability of individuals to engage in joint motor imitation using the ‘mirror game.’ In the ‘mirror game,’ an experimental paradigm based on a theater practice, two people were asked to create novel synchronous motion. Noy et al. (2011) made precise measures of players’ temporal and spatial coordination, contrasting actors and musicians who were experts at improvisation, with novices. Experts were able to generate highly synchronous (to less than 40 milliseconds) novel movements and, importantly, synchrony was greater during joint improvisation than when one individual was assigned a leader role and the other was instructed to copy the leader's movements. The performance of novices was relatively poor but improved with practice (Noy et al., 2011; Gueugnon et al., 2016).

Mutual or 'joint' motor imitation provides a unifying explanation for dolphin synchrony, including typical side-by-side synchs, as well as the complex displays. The enhanced performance of humans in the 'joint imitation' compared to the 'leader-follower' condition may explain the lack of leadership in dolphin synchrony. The inability of Herman (2002) to find leaders in novel synchronous behaviors suggests that his dolphins were playing the mirror game. If the signal value of synchrony (e.g. alliance unity) is based on timing precision, it would be counterproductive for a dominant individual to express leadership in that context (i.e., because the dominant individual would incur little or no consensus cost, cf Conradt & Roper, 2005). The importance of practice and expertise in 'joint' imitation makes biological sense if male dolphins use synchrony to gauge their compatibility with potential allies, as an advertisement of their alliance to others, and/or to impress choosy females. We caution that both mutual motor imitation and entrainment involve movement prediction so the relationship between the two phenomena remains to be clarified. The work of Herman (2002) on novel synchronous behavior and Jaakkola et al. (2018) on cooperation demonstrate that studies examining dolphin synchrony using the mirror game paradigm, particularly comparing their performance in the joint imitation versus follow-the-leader protocols, are eminently practical.

The second variable we studied was degree of synchrony. The degree of synchrony was not predicted by behavioral state, presence of consorted females, or differences in consortship rate within dyads. However, the members of the large WC 2nd-order alliance were more synchronous than individuals in the small RH 2nd-order alliance and, against our expectations, we found that closer associates within 2nd-order alliances were less synchronous.

We examined observer bias as a potential explanation for this unexpected relationship by comparing our measure of level of association between males (HWI) and the probability that a synch was not called in the field, and found that while fewer synchs by dyads with high association levels were missed, this was not statistically significant (see SI). In addition, the degree of synchrony for synchs only scored on video versus those also called in the field did not differ dramatically (see SI). Therefore, our finding of an inverse relationship between HWI and degree of synchrony may reveal that synchs between males that associate with each other less often are used as a way to reinforce or even strengthen 2nd-order alliance bonds that are less secure than bonds between frequent associates (see Zahavi, 1977). Thus WC males, which exhibited less stable 1st-order alliances, with males often switching partners between consortships, were more synchronous than males in the stable RH 1st-order alliances. This idea is also in keeping with the suggestion of Wilson & Cook (2016) that in cognitively sophisticated animals, attention and motivation may play an important role in successful entrainment. Motivation could be controlled in captive studies that examine dolphins' ability to entrain and engage in joint imitation.

Connor (2007) was puzzled by why movement synchrony was such an important alliance signal in dolphins and humans but not in alliance and coalition forming non-human primates. Movement synchrony is not featured in the behavior of allied male chimpanzees or cercopithicene primates, where male and female coalitions are common (e.g. Cords, 2012). Connor (2007) explored three possibilities for this human - dolphin convergence in the use of synchrony as an alliance signal: an enhanced ability to 1) perceive motion, 2) imitate, and 3) benefit from signals associated with the greater uncertainty about alliance relationships they experience in large social networks with dynamic-fission-fusion grouping patterns. While the relationship uncertainty hypothesis (Connor, 2007) was not based on a specific proximate mechanism, it fits well with the idea that motivation is a key factor for entrainment (and, by extension, joint imitation) in species with voluntary control over the coupling of sensory and motor systems (Wilson & Cook, 2016). This is similar to the more recent 'intrinsic reward and rhythmic synchronization' hypothesis of Takeya et al. (2017), which holds that the capacity for predictive and tempo-flexible synchronization to a beat (whether visual or auditory) is widespread, but that only certain vocal learning species are intrinsically motivated to do it (although we are skeptical that coalition forming primates would lack such motivation).

A more basic challenge to non-human primates may be their typical quadrupedal locomotion. The isochronic beat generated by human bipedal locomotion, heard and felt as early as *in utero*, may have facilitated the development of rhythmic/musical abilities, including synchronous locomotion, in humans (Parncutt & Chuckrow, 2019; Larsson et al., 2019). Footfall patterns in quadrupeds are relatively complex, change with speed (Larsson et al., 2019;

Hildebrand, 1989) and are apparently more difficult for bipedal humans to perceive (e.g. Horvath et al., 2009). In addition to perceptual difficulty, the more complex and varying (with speed) patterns of quadrupedal locomotion would be much more difficult to imitate or entrain to. The single case of whole body entrainment in chimpanzees involved bipedal locomotion (Lameira et al., 2019). Dolphin locomotion, with simple up and down fluke motion, like human walking, produces a simple isochronous beat. Thus, the synchronous behaviors by dolphins in our study may have developed in the same way that synchronous locomotion developed in humans.

There are a few reports of vocal synchrony during ‘chorusing’ in non-human primates (see Wilson & Cook 2016) including male chimpanzees (Fedurek et al., 2013). The Shark Bay dolphin society shares key features with common chimpanzee social organization, grouping patterns, male alliance/coalition formation, and mating system (e.g. Connor et al., 1992a; Connor & Vollmer 2009). However, Ravignani et al. (2014) conclude that the cases of primate chorusing are based on temporal overlap rather than precise synchrony or ‘joint adherence to a common pulse.’ Thus, a comparison of chorusing in male chimpanzees with movement synchrony in dolphins is interesting insofar as both reflect male affiliation (as will a number of other behaviors) but less so with respect to the underlying mechanism. By analogy, it is much more common for dolphins to simply overlap at the surface with one or more dolphins (a surfacing takes approximately two seconds, Connor et al., 2006) than to emerge from the water synchronously. It is possible such surfacing overlap, like the temporal overlap that defines chimpanzee pant-hoot chorusing, reflects affiliation, but precise joint imitation or entrainment is not required to explain the behavior.

It is worth noting that dolphins, as well as fish, may use auditory as well as visual cues from movement in water to synchronize (Larsson & Abbott, 2018; Jaakkola et al., 2010). It follows that the acoustic component of synchronous movement in dolphins may be a key part of the signal. Humans can synchronize movement using visual stimuli alone (Richardson et al., 2007); future research should explore the sensory inputs required for dolphin synchrony. Synchronous movements in dolphins, like fish, may have evolved to reduce predation risk via the ‘confusion effect’ (e.g. Connor, 2000). If so, voluntary control may have allowed dolphins to execute an existing behavior in other contexts, such as alliance signaling.

Dolphins and other toothed whales cooperate in alliance formation, feeding, protection of infants, and other contexts (see Connor et al., 2000). Given recent empirical findings that link synchrony and cooperative behavior in humans (Wiltermuth & Heath, 2009; Valdesolo et al., 2010; Trainor & Cirelli, 2015), studies exploring a general link between cooperative (and pro-social) behavior and synchrony in dolphins would be profitable.

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Tables

Table 1. Linear mixed model fixed effects estimates for leadership share.

	Estimate	Std. err	2.5% CI	97.5% CI
intercept	0.510*	0.244	0.00944	0.969
HWI	-0.239	0.276	-0.760	0.328
WC vs. RH	-0.174	0.146	-0.460	0.102

*significant at the 0.05 level

Table 2. Linear mixed model fixed effects estimates for degree of synchrony measured in mean number of frames apart for each dyad during synchs.

	Estimate	Std. err	2.5% CI	97.5% CI
intercept	5.233*	2.338	0.759	9.71
HWI	5.376*	2.707	0.196	10.56
WC vs. RH	-0.529	0.986	-2.416	1.360

*significant at the 0.05 level.

Table 3. Linear mixed model fixed effects estimates for degree of synchrony (number of frames) in behavioral and consortship contexts. Behavior: Non-social (n=337); social (n=29), intense social (n=46); pops (n=28). Consortships: NF= no consorted female (n=91), WF= intra-alliance synch, consorted female present (n=258), WNF= intra-alliance synch, no consorted female (n=43), A1F= inter-alliance synch, female present with 1 male (n=18), A2F= inter-alliance synch, female present with both males (n=29), AFO=inter-alliance synch, female with other alliance present (n=1).

	Estimate	Std. err.	2.5% CI	97.5% CI
intercept	9.149*	0.734	7.779	10.532
Social *vs*. non-social	-0.7602	1.148	-3.003	1.453
intense social *vs*. non-	-0.856	0.945	-2.680	0.988
pops *vs*. non-social	1.5040	1.180	-0.748	3.832
WC *vs*. RH	-1.529*	0.628	-2.732	-0.321
WF vs. NF	0.565	0.737	-0.848	2.003
WNF vs. NF	0.465	1.096	-1.643	2.590
A1F vs. NF	-0.0337	1.542	-2.977	2.966
A2F vs. NF	0.673	1.306	-1.838	3.205
AFO vs. NF	-3.825	5.961	-15.337	7.799

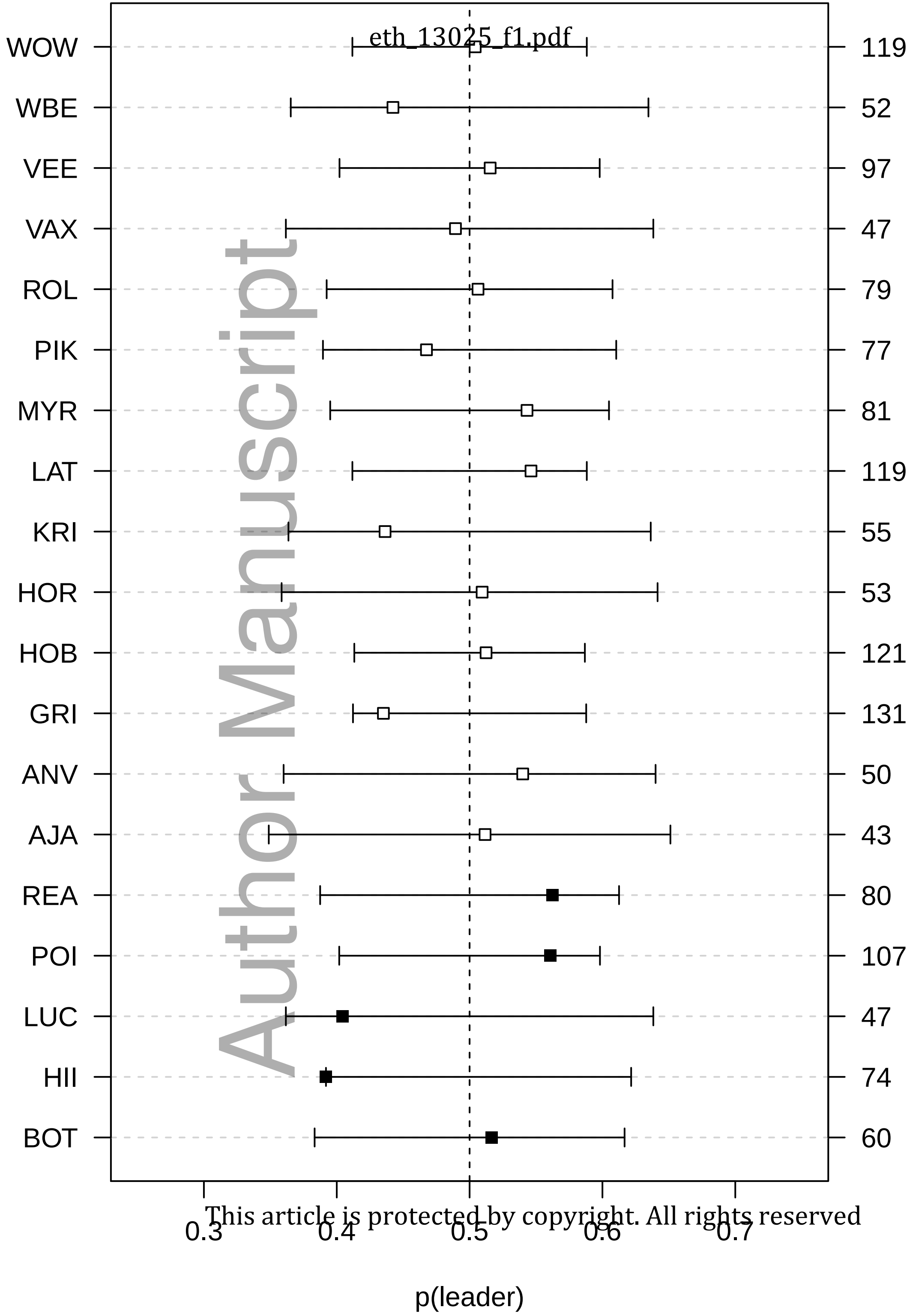
*significant at the 0.05 level

Figure legends

Figure 1. Proportion of synchs in which an individual was a leader. An observed value of

0.5 indicates that an individual is a leader as often as a follower across all synchs. Left y-axis indicates 3 letter codes for individual males. Right y-axis shows number of synchs included in calculations. Error bars show 95% simulated uncertainty intervals. Open squares indicate males from the WC 2nd-order alliance, closed squares are from the RH 2nd-order alliance.

Figure 2. Relationship between the mean number of frames apart (head) for each dyad with at least 5 synchs and their association index (HWI). Size of point is proportional to the sample size, which generated the mean (Range = [5-56]). Shaded = RH, Clear = WC.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