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Investigating the function of play bows in adult pet dogs (*Canis lupus familiaris*)

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ABSTRACT

Play bows are a common, highly stereotyped canine behavior widely considered to be a 'play signal,' but only one study has researched their function. Bekoff (1995) found that play bows function as behavioral modifiers to help clarify playful intent before or after easily misinterpretable behaviors, such as bite-shakes. To further examine the function of play bows, the current study analyzed five types of behaviors displayed by the bower and the partner immediately before and after a play bow during dyadic play. We found that play bows most often occurred after a brief pause in play. Synchronous behaviors by the bower and the partner, or vulnerable/escape behaviors by the bower (such as running away) and complementary offensive behaviors by the partner (such as chasing) occurred most often after the play bow. These results indicate that during adult dog dyadic play, play bows function to reinitiate play after a pause rather than to mediate offensive or ambiguous actions.

1. Introduction

Despite over 50 years of research on nonhuman animal play (hereafter animal play), researchers have yet to reach consensus on how to define this eclectic behavior. While easily determinable to observers (i.e., they know play when they see it) (Darling, 1937; Bekoff, 1995; Burghardt, 2005), defining play is problematic due to extensive variation in its behavioral components and seeming lack of adaptive function (Lorenz, 1956; Rosenberg, 1990; Bekoff and Allen, 1998). As animal play research has become more systematic and comparative, it has become increasingly clear that play behavior is not easily generalizable and varies dramatically across species (Pellis, 1993; Pellis and Pellis 1998; Bekoff, 1995; Palagi, 2006). During play, different species emphasize different motor patterns (Watson and Croft, 1996; Thompson, 1998), arrange these patterns into different sequences (Palagi, 2006) and employ unique behaviors or "play signals" to invite and/or maintain play (Loizos, 1967; Bekoff, 1976; Bekoff and Byers, 1981; Fagen, 1981; Ch.2; Palagi et al., 2015a,b).

Researchers have therefore proposed a wide variety of potentially adaptive benefits for social play (Baldwin and Baldwin, 1977; Poirier et al., 1978; Fagen, 1981; Lewis, 1982; Byers and Walker, 1995; Brown, 1998; Dolhinow, 1999; Spinka et al., 2001). Since across species play is typically more common in young adults and juveniles, it may function to develop motor abilities or hunting behaviors for future use (Fagen, 1981; Martin and Caro, 1985; Enomoto, 1990; Pellis and Iwaniuk, 2000; Burghardt, 2005). On the other hand, social play often utilizes play fighting, thereby borrowing behaviors shown during real fights, such as chasing, running and wrestling, potentially providing participants with a cost effective way to establish dominance or reinforce/test social bonds without engaging in an actual dispute (Bekoff, 1974; Aldis, 1975; Owens, 1975; Zahavi, 1977; Fagen, 1981; Paquette, 1994; Bekoff, 1995; Pellis and Pellis, 1996; Bekoff and Allen, 1998; Pellis and Iwaniuk, 2000; Bekoff et al., 2002; Burghardt, 2005).

Irrespective of the lack of consensus on its definition or function, play clearly involves communication between participants. Participants have to communicate their motivation in initiating play and negotiating the nature of their play interactions (Fagen, 1981; Pellis and Pellis 1996; Bekoff, 2001). Researchers have suggested that participants do this frequently through the use of *play signals*, which are generally used to commence, continue and recommence social play (Bekoff, 1972; Fagen, 1981; Smith, 1982; Palagi et al., 2015a,b). Such communicative skills typically develop during early social interactions and allow playmates to discern playful from non-playful scenarios (Bekoff, 1974; Horowitz, 2009). This communication employs bodily movements, vocalizations and facial expressions (Darwin, 1872; Rheingold, 1963; Fox, 1970; Bekoff, 1972).

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Table 1
Demographic data of domestic dogs sampled.

Name	Age during study (months)	Breed	Sex	Avg. weight (kg)	Housemates[b]
Abby (AB)	12[a]	Labrador Retriever	F	24.5	Mitch
Bahati (BA)	7–33, 144–156	Unknown mix	F	20.4	Safi, Tex, Lela*, Bentley
Bentley (BE)	12–40	Golden retriever mix	M	21	Tex, Lela*, Bahati
Bodhi (BO)	72[a]	German Shepherd	M	38	
Kobe (KO)	16–27	Unknown mix	F	28.1	
Lela (LE)	4–10	German Shepherd	F	13	Tex, Bahati*, Bentley*
Lucy (LU)	8–39	Keeshond/Shepherd mix	F	14.5	
Mitch (MI)	26–57	Labrador Retriever	M	34.5	Abby
Raven (RA)	23–42	Siberian Husky	M	23.1	
Rascal (RAS)	24[a]	Unknown mix	M	22	
Safi (SA)	108–146	German Shepherd	F	34.5	Bahati
Sullivan (SU)	12[a]	Pit bull mix	M	20	
Tasha (TA)	60[a]	Husky mix	F	22	
Tex (TX)	12–100	Belgian Tervuren mix	M	24	Lela*, Bahati, Bentley
Tuna (TU)	48[a]	German Shepherd	F	32	
Zoe (ZO)	15[a]	Standard Poodle	F	20	

[a] Subjects without an age span include data from a period of one year or less.
[b] Housemates reflect the other individuals a dog lived with over their lifetime. An * reflects a living arrangement of less than 1.5 years at the time the data were collected.

Table 2
Ethogram of behavior codes organized by behavior categories.

Vulnerable/escape	Offensive	Synchronous	Miscellaneous	Pause
Receives bite	Bites move	Mutual rear up	Close approach	Relatively stationary
	Bite still	Moves together	Chin-over move	Sitting
Receives muzzle bite	Bite muzzle		Chin-over stationary	Lying down
Runaway	Charge		Close non directional movement	
	Chase		Far non directional movement	
Being forced down	Force down		Move away	
Receives genital sniff	Gives genital sniff		Partial approach	
Receives mount	Mount		Play bow*	
Receives nip	Nip move		Play face	
	Nip still		Out of view	
Receives push/tackle	Push/tackle			
	Failed tackle			
Voluntary down				
Gives muzzle lick	Receives muzzle Lick			
Receives overs during downs	Overs during downs			

* See S7.

Domestic dogs (*Canis lupus familiaris*, hereafter referred to as dog) are unusual in that they exhibit high frequencies of play behaviors even as adults (Rooney et al., 2000; for a review of dog play see Bradshaw et al., 2015). Unlike play in other domestic carnivores such as cats (Hall, 1998; Hall et al., 2002) play in domestic dogs often involves a conspecific or human partner, suggesting that the underlying motivations are likely social (Rooney et al., 2000; Ward et al., 2008). Therefore, dog play signals are of considerable significance.

One of the most stereotyped play behaviors, the play bow (Darwin, 1872), is consistently found within dog play, in addition to other closely related species like coyotes, wolves, foxes and even lions (Bekoff, 1974; Schaller, 1972). Play bows can be identified by the high-rump crouch position, which occurs when the forequarters of an individual are bent, often in a lying down position, while the hindquarters remain elevated. Though this behavior is widespread and easily recognizable, its function within play has rarely been addressed scientifically.

Bekoff (1995) conducted the first detailed study on the function of play bows in canines. He observed that play bows were more likely to occur in association with behaviors that could potentially be misinterpreted as aggressive. Specifically, in a cross-species sample of domestic dogs (both infants and adults), infant gray wolves, and infant coyotes, bite-shakes were the most common behavior shown immediately before or after play bows (Bekoff, 1995). Bite-shakes are typically defined as one animal biting down on a play partner's head or neck and rapidly shaking his or her own head side to side. Therefore, Bekoff hypothesized that canines use play bows to reinforce ongoing social play and to clarify the bower's intentions so as to maintain a playful atmosphere (Bekoff, 1972, 1995).

Bekoff's (1995) domestic dog subjects included 4 infants (with observations taken over the period from 3 to 7 weeks of age) as well as 10 adults. The data from both age groups were combined, but it was not indicated how many observations from each contributed to the analysis. This is an unfortunate omission, since bite-shakes are rarely observed in adult domestic dogs (Ward et al., 2008). When analyzing play data during three stages, 3–8, 10–23 and 27–40 weeks of age, Ward et al. (2008) found that, as puppies from different litters developed, bite-shakes decreased drastically in frequency. Observed at their highest frequency of 13% (of all offensive plus self-handicapping behaviors shown during play) during weeks 3–8, bite-shakes dropped to 4% during weeks 10–23, and weren't seen at all during weeks 27–40 (Ward et al., 2008). Thus, Bekoff's (1995) conclusion about the clarifying function of play bows seems to apply only to infant (and maybe occasionally juvenile) dog play.

Furthermore, play bows have consistently been found to occur in association with non-aggressive behaviors rather than aggressive ones. During adult dog social play, within pair play bows were most frequently exhibited by individuals who self-handicapped (i.e., restrained full force or put themselves in vulnerable positions) more often, not by those who showed more offensive (i.e., mock-attack) behaviors (Bauer and Smuts, 2007). Ward et al. (2008) replicated these findings in young littermates.

Since the publication of Bekoff's (1995) paper, researchers have proposed additional functions for dog play bows. An untested hypothesis developed by Pellis and Pellis (1996) suggests that play bows may in fact not be play signals at all. Instead, bending the forequarters while maintaining elevated hindquarters might represent a highly strategic physical position that allows the bower to better escape from, or launch a mock-attack on, the play partner.

An alternative strategic function for play bows might involve communicating or developing common motivations. Play bows are occasionally performed synchronously or in association with other synchronous behaviors (i.e., the same behavior performed in unison between two individuals). These coordinated actions may indicate cooperative motivation(s) and/or the ability of individuals to function well as partners in a joint enterprise (Smuts, 1999). Consistent with this idea, Palagi et al. (2015a,b) recently documented the existence of play bow mimicry in dogs and showed that playmates who had known each other the longest showed the most mimicry. Thus, behavioral synchrony during play may occur in dyads with the common goal to continue a play bout and/or to further develop their relationship (Smuts, 2014).

While the function of play bows has not received much scientific attention, evidence suggests that they can be considered as visual signals. In dyadic dog play, play bows, as well as other assumed visual play signals, nearly always occurred when the pair faced one another after a brief pause (Horowitz, 2009). In addition, "attention-getting" behaviors were more common when play partners were facing away, and matched the receiver's degree of inattentiveness (Horowitz, 2009). Thus, the weaker the receiver's attentiveness, the stronger the sender's attention-getting behavior, suggesting that the play bower possesses some understanding of the positioning of his or her partner, and the circumstances in which it is appropriate to bow.

Due to the paucity of research and lack of consensus about the function of play bows in dog social play, the current study undertook to clarify the purpose of this highly stereotyped play signal. In doing so we attempted to replicate and/or test the four hypotheses discussed above: clarification of intentions, resumption of play, occupying a better strategic position, or synchronizing actions to develop a relationship (Bekoff, 1995; Pellis and Pellis, 1996; Smuts, 2014). While these hypotheses differ in their explanation of the play bow's function, all have identified strategic purposes. Some or all of these purposes may prove important, since play bows may be flexible, functioning differently across diverse play situations. Another aim of this research is to replicate Horowitz's (2009) finding that play bows are usually exhibited to a partner who can see the signal.

1.1. Hypotheses and predictions

To further examine the function of play bows in domestic dogs and identify consistent behaviors surrounding the performance of play bows, behaviors occurring just before and just after the play bow for both the play bower and the play partner were analyzed. The following hypotheses derive from the studies described above and predict outcomes that may not be mutually exclusive (hypothesis 1, 2 and 5), while others may be (hypotheses 2 and 3).

Hypothesis 1. Re-initiation of play

If play bows function to reinitiate play after a pause, both the bower and the partner should perform more pauses and passive non-play behaviors before the play bow than after.

Hypothesis 2. Clarification of easily misinterpretable behaviors

If play bows function to clarify behaviors most susceptible to misinterpretation, the bower should perform more offensive behaviors than the partner before and/or after play bowing.

Hypothesis 3. Attacking and escaping the play partner

a If play bows function to obtain an optimal position to better 'attack' the play partner, the bower should perform more offensive behaviors after the play bow than before.
b If play bows function to obtain an optimal position to better 'escape' the play partner, the bower should perform more vulnerable/escape behaviors, such as runaway (S1), after the play bow than before.

Hypothesis 4. Play bow synchronization

a If play bows function to help synchronize play behaviors, the bower and the partner should perform more synchronous behaviors after the play bow than before.

Hypothesis 5. Play bows as visual signals

a If play bows function as visual signals, play bows should be limited to times when the bower and partner are within one another's visual field (S2).
b If play bows function as visual signals, play bows performed when the players are not within one another's visual fields should occur in association with attention-getting behaviors, as defined by Horowitz (2009).

2. Materials and methods

2.1. Subjects

Subjects consisted of 16 well-socialized, spayed or neutered (except Lela) domestic pet dogs (Table 1). Age, breed, and sex varied across dyadic play partners (Table 1). All play interactions were between two adult dogs except for one subject, Lela, who was an adolescent. In order to eliminate the possibility of potential effects caused by including Lela in the sample, the data were analyzed without her. The results excluding play bows to Lela were identical to those presented here. Note that for these dyads, we only included adult bows *to* Lela (not by her) when she was between 4 to 7 months of age.

2.2. Data collection

2.2.1. Data collection and video coding

Dyadic play bouts were videotaped over a period of 10 years as part of a long-term study on dog play conducted by B. Smuts and colleagues. All footage analyzed for this study involved tapes previously recorded for research purposes. We analyzed only outside play, which typically occurred in large enclosed backyards or secluded public areas. The filmed dyads differed in their relationships as some consisted of new play partner interactions while others involved play between well-acquainted individuals.

Play bows were coded only when they occurred during a play bout (S4). A movement was coded as a play bow only when it met specific and detailed criteria that involved both the type of movement and its duration (S5). During a play bow, the pair was considered to be facing one another when both were within the other's visual field (S2). Occasionally, play bows performed by the bower and the partner overlapped in time and were considered to be synchronous bows (S6). In other words, if the second dog began a play bow before the first dog stood back up, the bows were considered synchronous.

All of the above-mentioned hypotheses addressing the functions of play bows focus on: (1) how a play bow might alter the partner's 'perception' of bower behaviors occurring right before or after the

bow (e.g., hypothesis 2), or (2) how the bow might reflect what occurred right before it and/or influence what occurred right after it, (e.g., hypotheses 1, 3a, 3b and 4). These hypotheses can be evaluated by: (1) recording specific behaviors shown by both dogs right before and after the bow and (2) determining whether these behaviors differ as a function of who showed them (bower or partner) and when they were shown (before or after the bow). The behaviors coded in association with play bows are listed and defined in S1).

The first two authors and one research assistant coded videos for 2 years (January 2013 to January 2015). Each coder underwent extensive training by the first author to learn the coding protocol. All three researchers coded the same videos independently until agreement of 90% was reached on the behaviors. After inter-observer reliability reached this standard, the three researchers coded different videos independently of one another.

2.2.2. Behavioral definitions

The first author, in collaboration with B. Smuts and R. Stokes, developed an ethogram based on previous studies, which included all of the primary behaviors seen during adult dyadic play (Bauer and Smuts, 2007; Ward et al., 2008). Play behaviors (from here on termed behavior codes) were then divided into 5 mutually exclusive categories: offensive, vulnerable/escape, pause, synchronous, and miscellaneous (Table 2, S3). Behavior categories were determined by combining behavior codes of similar types. Offensive behaviors (Ward et al., 2008) consisted of mock-attack play behaviors (e.g., tackle) and chases/charges. Vulnerable/escape behaviors included self-handicapping behaviors, receiving an offensive behavior (e.g., 'is tackled'), and running away behaviors, which could function as escapes from the partner. Pause behaviors were all behaviors that involved little movement (i.e., the dog took two steps or less). Synchronous behaviors included two predefined behavioral states, mutual rear-ups and move together, that two players sometimes performed in precise synchrony (e.g., they displayed one of these two behaviors in unison) (S1, S6). Lastly, miscellaneous behaviors consisted of behaviors that did not fall into any of the other categories. These included communicative behaviors, such as bowing (because a play bow could be immediately preceded or followed by another play bow) or showing a play face, and behaviors (e.g., chin-overs and approaches) that can be considered to be either mock-attacks or affiliation (especially courtship), depending on the context (Trisko and Smuts, 2015).

2.3. Data analysis

Analysis was conducted on 414 play bows by 16 dogs, including 10 females and 6 males over 229 recorded play bouts. These dogs played in 22 pairs, 9 female–female dyads, 10 male-female dyads and 3 male–male dyads (Table 3). To evaluate hypotheses 1 through 5, we used a generalized linear mixed model (GLMM) (Molenberghs and Verbeke, 2005) to analyze the proportion of a particular behavior category (Table 2) relative to all other behavior categories combined (binary model). The dependent variable for each GLMM is the proportion of behaviors in the behavioral category of interest modeled as:

$$P = \frac{a}{a+b+c+d+e}$$

Where a represents the number of behaviors in the behavior category of interest, and b, c, d, and e represent the number of behaviors in the other four behavior categories. For example, if category a, the numerator, equals the number of all offensive behaviors, then the denominator is a plus the number of behaviors falling into the other four behavior categories (vulnerable/escape behaviors, synchronous behaviors, pause behaviors and miscellaneous behaviors). For four out of the five behavior categories we were interested in how this proportion, the dependent variable, might compare as a function of role (bower's behavior vs. partner's behavior), timing (whether the behavior occurred before vs. after the bow), and the interaction of role and timing. While the miscellaneous behavior category was included in the analysis, we do not address it further because behaviors in this category were not directly relevant to any of our hypotheses.

Table 3
Play bows by dyad.

Dyad	Play bow count[a]	Mean bow[b]	Play bow ratio[c]
BA/LE	1	0.24	0:1
BA/LU	42	10.14	7:35
BA/SA	7	2.42	1:6
BA/RAS	4	0.97	2:2
BA/RA	2	0.48	2:2
BE/BA	1	0.24	1:0
BE/LE	61	14.73	41:20
KO/AB	1	0.24	1:0
KO/BA	1	0.24	1:0
KO/SA	2	0.48	2:0
LE/ZO	4	0.97	3:1
LU/SA	7	1.69	6:1
MI/SA	1	0.24	1:0
RA/AB	3	0.72	3:0
RA/MI	5	1.21	5:0
RA/SA	1	0.24	1:0
TU/BO	22	5.31	12:10
TX/BA	10	2.42	4:6
TX/BE	96	23.19	88:8
TX/LE	117	28.26	77:20
TX/SU	5	1.21	4:1
TX/TA	8	1.93	6:2

[a] The number of play bows performed by the dyad.
[b] The mean of all play bows performed by the dyad.
[c] The number of play bows within the dyad separated by individual. The first value corresponds to the number of play bows performed by the first dog in the corresponding "dyad" column. The second value corresponds to the number of play bows performed by the second dog in the corresponding "dyad" column.

Thus, the proportion of a given behavior (P) is modeled as:

$$\text{Logit}\left(P_{rtij}\right) = \beta_0 + \beta_1 \text{Role} + \beta_2 \text{Time} + \beta_3 (\text{Role} \times \text{Time}) + b_{0i} + b_{0ij}$$

where r denotes the role, t denotes timing, i denotes the individual dog, j denotes the dyad and b denotes a random effect. The model contained fixed effects for role (bower *vs.* partner) and timing (before *vs.* after the bow), and a fixed effect interaction between role and timing. Random effects for individual and dyad were included. Convergence criteria were satisfied for each test conducted.

Four separate binary regressions were run comparing one behavior category to all other behavior categories. Results therefore, represent the change in proportion of a particular behavior category across time (i.e., before or after the bow) and/or as a function of role (i.e., bower or partner). Since 4 comparisons, 2 for role and 2 for time, were used per behavior category analysis, a Bonferonni post-hoc correction of 0.01 was applied to results for each regression to reduce the chances of a type I error. Note that for the category synchronous behavior only two tests are reported since, by definition, the bower and the partner's behavior were required to be identical.

3. Results and discussion

The number of play bows per dyad varied considerably across pairs from 1 to 117 (Table 3). Four dyads, two male-female, one male-male, and one female–female accounted for 3/4ths of the play bows observed (316/414). No other pair accounted for more than 5.31% of the play bows. No obvious trends were apparent when analyzing whether the likelihood of play bowing was influenced by

sex, age, size or dominance, but sample sizes were inadequate for statistical analysis. Play bows lasted 2.25 s on average (n = 414). The shortest length recorded was 0.33 s (the minimum time required to consider the behavior a play bow, S5), while the longest bow lasted 4.68 s.

3.1. Hypothesis testing

Fig. 1 shows the proportion of all behaviors accounted for by each of the behavior categories (vulnerable/escape, offensive, synchronous, pause and miscellaneous) for both the bower and partner immediately before and after the bow. Table 4 shows whether such proportions were significantly different as a function of timing (before vs. after the bow) and role (behavior by the bower vs. the partner. The fixed effects interaction for role by timing was not significant for any GLMM behavior category proportions ($p \geq 0.23$).

3.1.1. Hypothesis 1: re-initiation of play

Hypothesis 1 predicted that both the bower and the partner would show more pause behaviors before the play bow than after. Results confirmed this prediction (Table 4, row 1, columns A and B). The fact that bowers and partners showed proportionately more active behaviors after the play bow than before suggests that play bows often functioned to stimulate play after a pause (S8, S9). Horowitz (2009) observed similar trends in dog play, noting that play signals occurred more frequently after pauses.

3.1.2. Hypothesis 2: clarifying easily misinterpretable behaviors

Hypothesis 2 based on Bekoff's (1995) findings, predicted that if play bows function to clarify easily misinterpretable behaviors, bowers should perform more offensive behaviors before and/or after play bows than partners. There was no difference in offensive behaviors by role, either before or after the play bow (Table 4, row 3, columns C, D). In fact, partners, not bowers, were more likely to perform offensive behaviors after the play bow than before (Table 4, row 3, column B).

Bekoff (1995) found that play bows occurred most often in association with bite-shakes by the bower. We never observed bite shakes before or after play bows by either the bower or the partner, but we recorded bite-like actions (e.g., nips and bites, hereafter called bites). Of the 1656 behaviors recorded for both the bower and the partner before and after the bow, only 99 (5.97%) were bites. The bower and partner performed similar proportions of bites (53/99 and 46/99 respectively). The bower performed similar numbers of bites before (n = 27) and after the bow (n = 26). The partner, in contrast, appeared more likely to bite after the bow (n = 34) than before (n = 12). These descriptive findings provide no support for the idea that adult dogs used bows to clarify their intentions around biting behaviors. Recall that many of the subjects in Bekoff's (1995) study were infant dogs (age 3–7 weeks). Thus, our findings indicate that play bows may function quite differently during infant–infant interactions than they do among adult dogs. However, further research is needed to evaluate this conclusion, since our results and those of Bekoff (1995) cannot be directly compared due to methodological differences. Specifically, we focused on the behaviors occurring immediately before and after the play bow for both playing individuals, whereas Bekoff (1995) analyzed the frequencies of various behaviors throughout play bouts to determine which ones (e.g., bite-shakes) occurred more often in association with play bows than expected by chance.

3.1.3. Hypothesis: attacking & escaping the play partner

Hypothesis 3a proposed that play bows might function to better position the bower to 'attack' the play partner. If so, bowers should perform more offensive behaviors after the play bow than before. However, as noted above (hypothesis 2), bowers did not show higher proportions of offensive behaviors after the bow than before (Table 4, row 3, column A). In fact the opposite was found, as play partners, rather than bowers, showed significantly higher proportions of offensive behaviors after a play bow than before (Table 4, row 3, column B). Thus, no support was found for hypothesis 3a of the two-part hypothesis set forth by Pellis and Pellis (1996).

Hypothesis 3b alternatively suggested that play bows might function to better position the bower to escape from the play partner. If so, bowers would be expected to perform more vulnerable/escape behaviors after the play bow than before. This prediction was confirmed (Table 4, row 2, column A). Bowers were also more likely to perform vulnerable/escape behaviors after the play bow than were their play partners (Table 4, row 2, column D), an effect of role consistent with hypothesis 3b but not predicted by it.

Although these findings can be interpreted as support for hypothesis 3b, we think another interpretation is more plausible. If play bows functioned as a means for the bower to escape play partners, one would expect to see a high proportion of offensive behaviors by the partner before the play bow; that is, a high proportion of behaviors that the bower needed to escape from. Instead, the partner performed more offensive behaviors *after* the play bow than before. In addition, many of the escape-like behaviors shown by the bower after the bow resulted in chases by the partner. Rapidly running away after bowing perhaps helped to call the partner's attention to an invitation to chase and thus functioned to initiate a particularly active play sequence.

3.1.4. Hypothesis 4: play bow synchronization

Hypothesis 4a predicted that if play bows help a pair to synchronize their behaviors, then synchronous behaviors should be more common after a play bow than before. Since, by definition, the proportion of synchronous behaviors must always be the same for the bower and the partner, one statistical test applies to both roles. The prediction was confirmed: bowers and partners performed higher proportions of synchronous behaviors after the play bow than before (Table 4, row 5, column A).

These results suggest that play bows in general may help partners to synchronize behaviors (S10, S11). Additionally, Palagi et al. (2015a,b) showed that play sessions with play bow mimicry (similar to play bow synchrony in this study) lasted longer than sessions without such mimicry. Play bow synchrony/mimicry may increase bout length by communicating a desire to continue playing (Palagi et al., 2015a,b). Whether synchronous or mimicked behaviors during play actually enable play partners to better coordinate mutually beneficial behaviors or simply occur more often in dyads that are already especially in tune requires further investigation. Whether synchronous behaviors actually enable play partners to better coordinate mutually beneficial behaviors or simply occur more often in dyads that are already especially in tune requires further investigation.

3.1.5. Hypothesis 5: play bows as visual signals

Hypothesis 5a predicted that play bows would almost always be limited to times when the bower and partner were within one another's visual field. This prediction was confirmed: for 409 of the 414 play bows the dogs could see one another.

In these five exceptional instances, play bows were expected to be associated with attention-getting behaviors, as defined by Horowitz (2009) (hypothesis 5b). Although the sample is very small, our observations support Horowitz (2009). For one of these bows, due to the camera angle we could not determine whether the dogs could see one another. In three of the remaining four play bows without mutual visual attention, the bower barked (i.e., an attention getting behavior) during the bow. Thus out of 413 bows, only once did neither mutual visual attention nor barks occur. This sug-

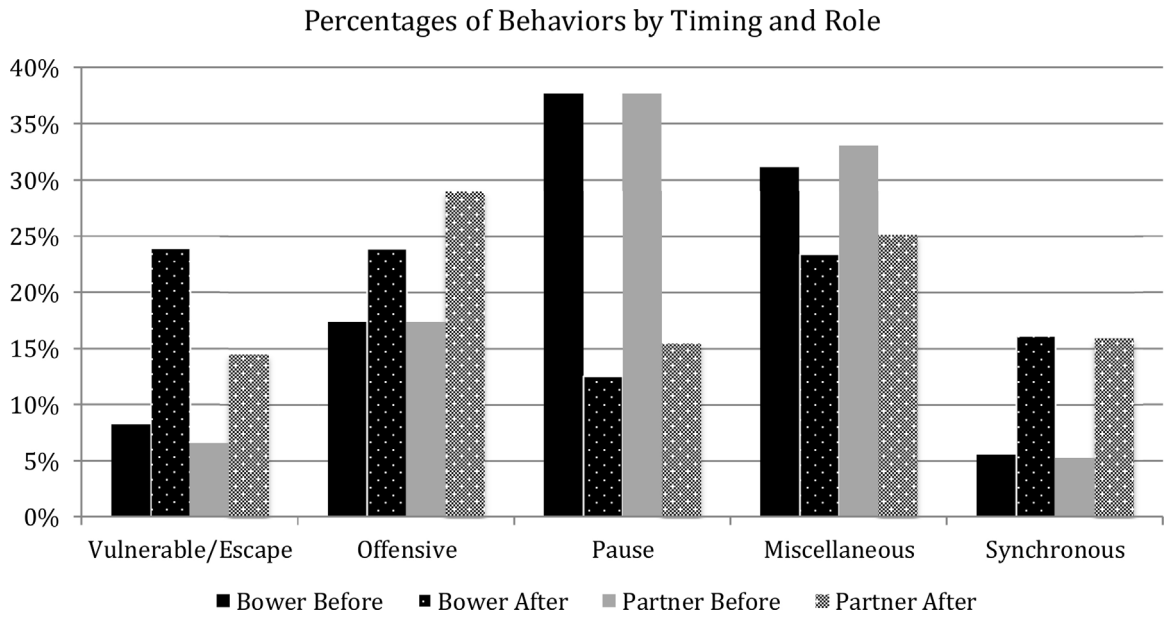

Fig. 1. The percentage of behaviors in each behavior category observed for both the bower and partner before and after the play bow.

Table 4
General linear mixed model results.

	Timing		Role	
Behavior categories	Before vs. after for bower	Before vs. after for partner	Bower vs. partner before	Bower vs. partner after
Pause	**p < 0 .0001**	**p < 0.0001**	p = 0.7421	p = 0.1885
Vulnerable/escape	p < 0.0001[a]	p = 0.0003[1]	p = 0.1818	p < 0.0001[1]
Offensive	p = 0.0194	p = < 0.0001[1]	p = 0.8606	p = 0.1484
Miscellaneous	p = 0.0124	p = 0.0113	p = 0.5153	p = 0.5403
Synchronous	**p = 0.0001**[b]		p = 1.000[2]	

Bold face—significant results in predicted direction.
[a] Significant results that were not predicted.
[b] There is only one corresponding p-value because the statistical tests are identical.

gests that play bowers understand when it is and is not appropriate to use a bow as a visual signal.

4. General conclusions

In order to address the function of play bows within adult dog dyadic play, we analyzed the behaviors occurring immediately before and after a bow for both the play bower and play partner. To our knowledge, only one other study (Bekoff 1995) has examined the function of play bows in domestic dogs. Although Bekoff found that bowers were most likely to show bite-shakes before and after bowing, we did not observe any bite-shakes in association with bowing by either the bower or the partner, suggesting that Bekoff's finding may apply mainly, or only, to infant dog play. Our analysis of offensive behaviors (e.g., bites and nips without head-shakes, tackles, charges, etc.) did not support Bekoff's (1995) hypothesis that play bows function as a means to clarify behaviors easily misinterpretable as aggression.

Differences between this study and Bekoff's (1995) lead to three additional hypotheses that deserve further investigation: (1) It is possible that play bows function differently within litters than they do between unrelated dogs, regardless of age. The puppies in Bekoff's study were littermates, whereas the dogs in this study were not related, although some pairs lived together; (2) Play bows may function differently when partners are placed together by the researcher, as was the case for the infant pairs in Bekoff's study. In this study, in contrast, many of the play partners were chosen by the dogs themselves in situations in which more than one partner was potentially available; and (3) Play bows may function differently when dogs are at liberty to play when they please, as in this study, whereas in Bekoff's study play sessions were arranged and observed at a set time every day.

This study focused only on the behaviors shown immediately before and after play bows, whereas Bekoff's (1995) study calculated frequencies of various behaviors throughout play bouts and then determined which ones (e.g., bite-shakes) occurred more often in association with play bows than expected by chance. A study employing methods similar to Bekoff's would allow a more direct comparison with his findings. However, methodological differences cannot explain away our finding that partners, rather than bowers, exhibited proportionately more offensive behaviors after a bow than before.

Lastly, a study across infant, juvenile, and adult play could determine how play bows function and develop. The disparities in previous research (Bekoff, 1995 vs. Bauer and Smuts, 2007 and Ward et al., 2008) in relation to how play bows function suggest that some of the variation may be due to age. Such a study could independently determine the frequency of bite-shakes during play among infant, juvenile and adult dogs, potentially allowing further testing of Bekoff's (1995) influential hypothesis.

Additionally, we aimed to investigate an untested hypothesis (Pellis and Pellis 1996) that play bows function to gain an optimal physical position from which one can better attack or escape from a play partner. Partners, rather than bowers, were more likely to perform offensive behaviors after play bows than before, rejecting the hypothesis that bowers use play bows to better launch

mock-attacks. However, bowers were more likely to perform vulnerable/escape behaviors (especially running away) after a play bow than beforehand, supporting the hypothesis by Pellis and Pellis (1996) that play bows function to favorably position the bower for an escape. However, the fact that both bowers and partners were often stationary before play bows and highly active after them (in the form of synchronous interactions or runaway/chase dynamics) supports the hypothesis that bows most often functioned to reinitiate play after a pause.

Taken together, these findings suggest that play bows do not occur at random and do not, therefore, simply enhance the play atmosphere in a general way. Instead, their association with particular behaviors before and after the play bow suggests strategic use of this play signal to accomplish immediate goals (Palagi et al., 2015a,b), including continuing play by enticing the partner into a synchronous or runaway/chase interaction, potentially prolonging the play bout. Whether these goals have anything to do with ultimate function, in the evolutionary sense, remains to be determined.

4.1. Limitations and future studies

While this study evaluated previous hypotheses addressing the function of play bows, future studies should attempt to replicate and extend these results. Approximately 75% of the 414 play bows we observed occurred within 4 different dyads, and 45% of bows were shown by one individual (190/414). Even though the general linear mixed model included random effects for individuals and dyads, a larger and less skewed dyadic sample could be more representative of the domestic dog population. Additionally, a larger sample would also allow researchers to analyze breed, sex, and age effects on play bow use to determine potential trends.

Future research should not only increase the sample size but should also distinguish between bows involving unfamiliar vs. familiar partners, since play bow usage could change as dogs become more familiar with their play partners. It would also be useful to study play bows within stable groups, including naturally occurring groups of free-ranging dogs in which most or all group members are sexually intact (e.g., Cafazzo et al., 2014). Studying stable groups is important because competition within a group for play partners might affect the use and function of play bows. For example, since play bows function as play signals to begin or maintain play, excess signaling may be used competitively when multiple dogs desire to play with a certain partner. Since dyadic play lacks such competition for preferred play partners, further research may uncover additional strategic functions of the play bow within group play.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.beproc.2016.02.007.

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