DOES LIFE HISTORY PREDICT RISK-TAKING BEHAVIOR OF WINTERING DABBLING DUCKS?

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Abstract. Life-history theory predicts that longer-lived, less fecund species should take fewer risks when exposed to predation than shorter-lived, more fecund species. We tested this prediction for seven species of dabbling ducks (*Anas*) by measuring the approach behavior (behavior of ducks when approaching potential landing sites) of 1099 duck flocks during 37 hunting trials and 491 flocks during 13 trials conducted immediately after the 1999–2000 waterfowl hunting season in California, USA. We also experimentally manipulated the attractiveness of the study site by using two decoy treatments: (1) traditional, stationary decoys only, and (2) traditional decoys in conjunction with a mechanical spinning-wing decoy. Approach behavior of ducks was strongly correlated with their life history. Minimum approach distance was negatively correlated with reproductive output during each decoy treatment and trial type. Similarly, the proportion of flocks taking risk (approaching landing sites to within 45 m) was positively correlated with reproductive output. We found similar patterns of approach behavior in relation to other life-history parameters (i.e., adult female body mass and annual adult female survival rate). Thus, species characterized by a slower life-history strategy (e.g., Northern Pintail [*A. acuta*]) were more risk-averse than species with a faster life-history strategy (e.g., Cinnamon Teal [*A. cyanoptera*]). Furthermore, although we were able to reduce risk-averseness using the spinning-wing decoy, we were unable to override the influence of life history on risk-taking behavior. Alternative explanations did not account for the observed correlation between approach behavior and life-history parameters. These results suggest that life history influences the risk-taking behavior of dabbling ducks and provide an explanation for the differential vulnerability of waterfowl to harvest.

Key words: allometry, Anas, *dabbling ducks, life history, predation risk, risk-taking behavior, spinning-wing decoy.*

¿Pueden las Historias de Vida Predecir el Comportamiento de Toma de Riesgos en los Patos del Género *Anas*?

Resumen. La teoría de las historias de vida predice que las especies más longevas y menos fecundas deberían tomar menos riesgos cuando son expuestas a depredación que las especies menos longevas y más fecundas. Evaluamos esta predicción en siete especies de patos del género *Anas* mediante la medición del comportamiento de acercamiento (comportamiento de los patos cuando se acercan a sitios de aterrizaje potenciales) de 1099 bandadas de patos durante 37 ensayos de cacería y 491 bandadas durante 13 ensayos desarrollados inmediatamente después de la estación de caza de aves acuáticas de 1999–2000 en California, Estados Unidos de América. También manipulamos experimental-mente qué tan atractivo resultaba el sitio de estudio mediante el uso de señuelos en dos tratamientos: (1) señuelos inmóviles tradicionales, y (2) señuelos tradicionales junto con un señuelo mecánico que bate las alas. El comportamiento de acercamiento de los patos se correlacionó fuertemente con su historia de vida. La distancia mínima de acercamiento se correlacionó negativamente con el rendimiento reproductivo durante cada tratamiento de señuelos y tipo de ensayo. De modo similar, la proporción de bandadas que tomó riesgos (acercándose a menos de 45 m de los sitios de aterrizaje) se correlacionó positivamente con el rendimiento reproductivo. Encontramos patrones similares de comportamiento de acercamiento en relación con otros parámetros de la historia de vida (i.e., masa corporal de las hembras adultas y tasa de supervivencia anual de las hembras adultas). Así, las especies caracterizadas por una estrategia de historia de vida más lenta (e.g., *A. acuta*) fueron más reacias a tomar riesgos que las especies con una estrategia de historia de vida más rápida. (e.g., *A. cyanoptera*). Además, aunque pudimos reducir el nivel de aversión a situaciones de riesgo usando el señuelo mecánico, no pudimos reemplazar la influencia

de la historia de vida en el comportamiento de toma de riesgos. Las explicaciones alternativas no aclararon la correlación observada entre el comportamiento de acercamiento y los parámetros de la historia de vida. Estos resultados sugieren que la historia de vida influencia el comportamiento de toma de riesgos de los patos del género *Anas* y brinda una explicación sobre la vulnerabilidad diferencial de la avifauna acuática a la cacería.

INTRODUCTION

Life-history theory predicts that longer-lived and less fecund species should take fewer risks when exposed to predation than shorter-lived and more fecund species (Roff 1992, Stearns 1992). This prediction is based on the underlying trade-off between the need to avoid predation and the benefits to be gained from engaging in a given activity, such as foraging or searching for mates (reviewed by Lima and Dill 1990). Efforts to test this prediction have focused on risk-taking behavior during the breeding season, due to the obvious trade-off parents must make between defense of their offspring and their own survival (Montgomerie and Weatherhead 1988). For example, longer-lived and less fecund species of both tropical-nesting passerines and temperate-nesting duck species tend to put themselves at less risk when defending their nests against predators than shorter-lived and more fecund species (Ricklefs 1977, Forbes et al. 1994).

Life history should also influence behavioral decisions made under the risk of predation during the nonbreeding season, yet few studies have examined such effects. The influence of life history on risk-taking behavior during the nonbreeding season might be especially prevalent in species subject to harvest, because a large proportion of annual mortality for these species occurs during the nonbreeding season. Thus, waterfowl are particularly appropriate subjects to conduct a comparative life-history analysis of risk-taking behavior during the nonbreeding season. Hunting accounts for approximately half of the total annual mortality in North American waterfowl populations (Bellrose 1976), has occurred for well over a century in North America, and hunting seasons can last for as long as 107 days per year (Baldassarre and Bolen 1994). It is thus reasonable to assume that hunting has acted as a selective agent on risk-taking behavior of waterfowl.

A common behavioral decision waterfowl must make under the risk of predation is whether to approach or avoid a potential landing site. This behavioral decision might be learned or innate, but in either case risk-taking behavior can be an evolved trait, because selection can act to reduce neophobia when ecological plasticity for site selection is favored (Greenberg 1984, Greenberg 1990). Because waterfowl travel between roosting and feeding sites daily (Fleskes et al. 2002) and migrate over thousands of miles each year (Bellrose 1976), they must rapidly assess the safety and profitability of many new landing sites. Waterfowl are highly gregarious and are strongly attracted to flocks of birds with which to feed, loaf, and engage in social behaviors (Baldassarre and Bolen 1994). However, approaching a potential landing site and its resources is also dangerous because of the possible presence of aerial or terrestrial predators, including human hunters using decoys to attract birds. Therefore, waterfowl are commonly faced with a trade-off between avoiding potentially dangerous sites and approaching sites to join conspecifics and acquire necessary resources (Pöysä 1987, 1991).

The amount of risk waterfowl will take when approaching a landing site (hereafter referred to as approach behavior) might depend on their life-history strategy. For example, shorter-lived and more fecund species (*r*-selected; MacArthur and Wilson 1967, Pianka 1970), i.e., those with a faster life-history strategy (Gaillard et al. 1989), have fewer breeding opportunities in the future compared to longer-lived and less fecund species (*K*-selected; MacArthur and Wilson 1967, Pianka 1970), i.e., those with a slower life-history strategy (Gaillard et al. 1989). Therefore, species with a faster life-history strategy should be selected to invest more heavily in current reproduction. For waterfowl, preparing for a reproductive episode begins well before the spring breeding season. Unlike many species of birds, pair formation in ducks occurs during the autumn and winter, and competition for females can be intense due to sex ratios skewed toward males (Bellrose et al. 1961, Bellrose 1976, Rohwer and Anderson 1988). In addition, food resources may become limiting

over winter (Heitmeyer 1989) and waterfowl must acquire sufficient nutrient and energy reserves to survive over winter, compete successfully for mates, and meet the energetic costs of migrating to distant breeding areas and laying large clutches (Heitmeyer and Fredrickson 1981, Krapu 1981, Haramis et al. 1986, Dubovsky and Kaminski 1994, Jeske et al. 1994). Therefore, selection for obtaining mates and nutrients may drive species with a faster life history to take more risks during the winter in preparation for the spring breeding season than species with a slower life history. The critical assumption is that behavior of dabbling ducks in winter affects their breeding performance the following spring. Although cross-season effects are difficult to detect, evidence suggests that conditions during winter can affect breeding success in spring (Heitmeyer and Fredrickson 1981, Raveling and Heitmeyer 1989).

Here, we examined whether approach behavior of dabbling ducks (*Anas* spp.) during the nonbreeding season was related to their life-history strategy. We did so under two environmental conditions: when the risk of human predation was high (on active hunts during the waterfowl hunting season) and when the risk of human predation was low (after the waterfowl hunting season). We predicted that longer-lived and less fecund species (e.g., Northern Pintail [*A. acuta*]) would be more risk-averse than shorter-lived and more fecund species (e.g., Cinnamon Teal [*A. cyanoptera*]).

In addition, we conducted a second experiment to determine whether we could override the influence of life history on the risk-taking behavior of dabbling ducks by manipulating the attractiveness of the study site. We used a novel spinning-wing decoy that has been shown to be a strong attractant to ducks and to increase harvest rates by 2.4 times over traditional decoy methods in North America (Caswell and Caswell 2004, Szymanski and Afton 2005, Ackerman et al. 2006). In effect, these decoys act as an exceptional stimulus and are used by hunters to attract ducks to come within shooting range. It is unclear whether ducks perceive sites with the spinning-wing decoy as having reduced predation risk, increased foraging and social benefits, or both. Nevertheless, spinning-wing decoys appear to reduce the perceived risk-to-reward ratio of sites more than traditional decoys alone, such that ducks

are more likely to approach a given location (Ackerman et al. 2006). We manipulated the attractiveness of the study site by using two decoy treatments during actual hunts and posthunting season observational trials: traditional decoys only versus traditional decoys with a spinning-wing decoy. Specifically, we tested four alternative hypotheses: (1) risk-taking behavior would not be related to life history under either decoy treatment (Fig. 1a), (2) risk-taking behavior would increase with faster life-history strategies, but there would be no effect of the spinning-wing decoy on risk-taking behavior (Fig. 1b), (3) risk-taking behavior would increase with faster life-history strategies and would be higher when the spinning-wing decoy was used (Fig. 1c), and (4) risk-taking behavior would increase for all species when the spinning-wing decoy was used, but the spinning-wing decoy would override the relationship between risk-taking behavior and life history such that life history would no longer be related to risk-taking behavior (Fig. 1d).

METHODS

SPECIES AND STUDY AREA

We studied seven congeneric species of dabbling ducks (Anatidae; *Anas*) that are common winter residents of the Central Valley of California: Northern Pintail (*A. acuta*), Mallard (*A. platyrhynchos*), American Wigeon (*A. americana*), Gadwall (*A. strepera*), Northern Shoveler (*A. clypeata*), American Green-winged Teal (*A. crecca*), and Cinnamon Teal (*A. cyanoptera*). These species are harvested heavily during the fall and winter hunting season in California.

We conducted our study during and immediately after the 1999–2000 waterfowl hunting season (16 October 1999 to 23 January 2000). About 20% of North America waterfowl overwinter in the Central Valley of California (Gilmer et al. 1982). We sampled both natural wetland and agricultural habitats throughout the Central Valley, including the predominant waterfowl wintering areas in the Sacramento Valley, Suisun Marsh, and San Joaquin Grasslands regions. All agricultural habitats were rice fields flooded after harvest, whereas natural areas consisted of a range of moist-soil habitats common to California's waterfowl refuges.
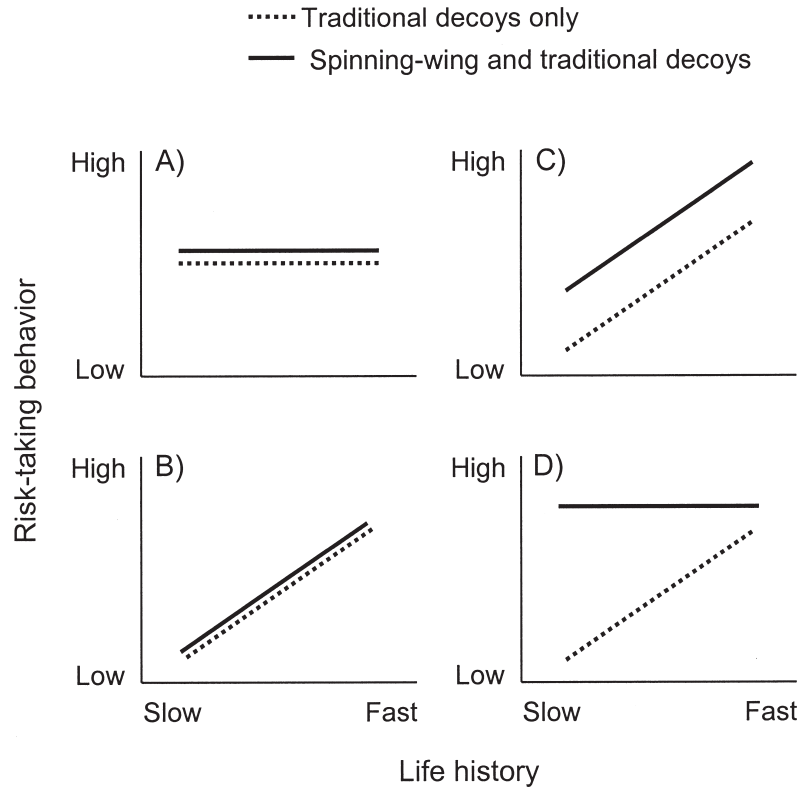
FIGURE 1. The potential relationships between risk-taking behavior and life history of dabbling ducks during normal hunting conditions (dashed line) and when the attractiveness of the site is experimentally increased using a spinning-wing decoy (solid line): (a) Risk-taking behavior is not correlated with life history under either decoy treatment; (b) Risk-taking behavior increases with faster life histories (shorter-lived and more fecund), but there is no effect of the spinning-wing decoy on risk-taking behavior; (c) Risk-taking behavior increases with faster life histories under both decoy treatments, and is greater when the spinning-wing decoy is used; and (d) Risk-taking behavior is greater when the spinning-wing decoy is used, but the spinning-wing decoy overrides the relationship between risk-taking behavior and life history such that life-history no longer influences risk-taking behavior.

LIFE-HISTORY PARAMETERS

We considered three life-history parameters (body mass, reproductive output, and annual survival rate) in our analyses to evaluate the robustness of the relationship between life history and risk-taking behavior in waterfowl. We used life-history data from adult females (following Krementz et al. 1997) because maternal mass is often highly correlated with reproductive characteristics (Blueweiss et al. 1978). Although dabbling ducks are sexually dimorphic in body size, adult female body mass is highly correlated with adult male body mass in the species used in this study ($r = 0.99$, $n = 7$, $P < 0.001$), and sex differences would have very little influence on the observed relationships.

We used body mass to index overall size because it explains a significant proportion of the variance in numerous life-history traits in vertebrates (reviewed by Blueweiss et al. 1978, Lindstedt and Calder 1981, Western and Ssemakula 1982, Sæther 1987, Stearns 1992). We used body masses obtained during winter only because female waterfowl experience large fluctuations in mass near the time of egg formation and incubation in the spring (Krementz et al. 1997). Body mass data were taken from Bellrose (1976), except when Dunning (1993) had larger sample sizes.

In addition, we used reproductive output (RO = mean clutch mass [g]/mean female mass [g]) as a more comprehensive life-history

parameter (following Forbes et al. 1994). Of the commonly used traits in life-history analyses, clutch size is known to exhibit a high degree of variation that is independent of body size in birds (Sæther 1987, 1988), including waterfowl (Laurila 1988). Hence, reproductive output provides a more inclusive life-history measure because it incorporates variation related to both body mass and clutch size in life-history traits. Clutch mass for each species was calculated by multiplying the mean clutch size (summarized by Bellrose 1976) by the mean egg mass (summarized by Rohwer 1988).

Lastly, we examined annual survival rate because it is a preferred parameter for comparative life-history analyses in waterfowl (Krementz et al. 1989) and, similar to clutch size, exhibits a high degree of variation that is independent of body size (Sæther 1987, 1989). Annual survival rate may have a more tangible relationship with risk-taking behavior than other life-history parameters, since increased risk-taking often results in immediate mortality. For each species, we averaged the annual survival rate estimates for adult females summarized by Krementz et al. (1997) for North America waterfowl; no estimate of annual survival was provided for Cinnamon Teal so we used an estimate from Gammonley (1996). We note that, although survival rates for waterfowl are among the most precise estimates available for wild vertebrates, better measurements exist for body mass and reproductive characteristics (i.e., clutch size and egg mass) than for annual survival rate (sensu Krementz et al. 1989). Thus, reproductive output is probably the best life-history parameter for comparative analyses among dabbling ducks.

RISK-TAKING BEHAVIORS

We used the minimum distance to which waterfowl flocks approached a landing site as our primary index of risk-taking behavior. Risk-taking behavior is commonly measured using the minimum distance to which an individual approaches a potential predator or allows a predator to approach. For example, the distance at which an incubating female flushes from her nest as a predator (e.g., an observer) approaches has been used in several studies to successfully investigate the parental investment behavior of waterfowl (Forbes et al. 1994, Sjöberg 1994, Mallory et al. 1998,

Gunness et al. 2001). Likewise, although sites with conspecific and heterospecific decoys are more likely to attract ducks than sites without decoys (Pöysä 1987, Pöysä et al. 1998), approaching a site is still a risky behavior for ducks because of the potential for the presence of predators, e.g., hunters. The probability of being killed by hunters increases for ducks the more closely they approach a site, because shooting success depends in large part upon a bird's distance from the hunter (Mikula et al. 1977, Humburg et al. 1982, Hebert et al. 1984).

As a second measure of risk-taking behavior, we used the proportion of flocks within 100 m that subsequently approached to within 45 m of the hunting blind. This measure is based on the assumption that all ducks within shotgun range (i.e., ≤45 m; Humburg et al. 1982) have a similar vulnerability to harvest because hunters may be equally successful in shooting a duck at 30 m as they would be at 20 m, since both distances are within shotgun range. This second index of risk-taking behavior also alleviates the concern that hunter behavior (i.e., the act of shooting) limits the minimum approach distance, since ducks might have approached even closer to the decoys if hunters had not deterred them by discharging their firearms. The proportion of flocks that approach to within 45 m is not influenced by hunter behavior since shooting at ducks rarely occurs at >45 m, and therefore may be a more appropriate index of risk-taking behavior for waterfowl during the hunting season.

BEHAVIORAL OBSERVATIONS

Hunting and posthunting season trials. We conducted 37 hunts from 16 October 1999 to 23 January 2000 during the waterfowl hunting season in California (hereafter hunting trials) and 13 observational trials from 27 January to 21 February 2000, after the waterfowl hunting season (hereafter observational trials). Fewer observational than hunting trials were conducted due to the shorter period of time available after the waterfowl hunting season and before the majority of waterfowl began migrating to the northern breeding grounds (late February).

Hunting trials differed from observational trials in that they were conducted with volunteer hunters, whereas observational trials simulated a hunting situation but no shooting

occurred. We contacted potential volunteer hunters by: (1) telephoning duck hunters drawn randomly from membership lists of waterfowl organizations in the state, and (2) writing to private duck-hunting clubs drawn randomly from club lists provided by state agencies.

For hunting trials, one observer accompanied each volunteer hunter and hunting partner to their duck-hunting club or other hunting location. For observational trials, one observer conducted the simulated hunts at duck-hunting clubs or waterfowl refuges. The observer sat either with the hunters in the blind or in the closest patch of vegetation. We encouraged the hunters to hunt, shoot, and otherwise behave as they would under normal hunting conditions. We did not direct or influence their shooting and tried to have as little influence on their hunting as possible. Each hunt began at legal hunting time (0.5 hr before dawn). In addition to similar decoy treatments (see below), both hunting and observational trials had experienced hunters using duck calls in addition to decoys in an attempt to entice waterfowl to the hunting location.

Decoy treatments. We used two decoy treatments within each hunting and observational trial: (1) traditional decoys only, and (2) traditional decoys and a mechanical spinning-wing decoy, the latter being a stronger duck attractant. For each of the first hunting and observational trials, we randomly determined the starting decoy treatment. In all subsequent trials, we systematically alternated the starting decoy treatments. After the starting treatment was determined, we systematically alternated the decoy treatment every 30 min until each hunter's bag limit (the number of ducks allowed to be harvested each day) was filled or six sampling periods (yielding three paired treatments) were completed. We allowed a minimum of 3 min between decoy treatments, during which no shooting was allowed, to separate each decoy treatment. Thus, each hunting and observational trial lasted 3 hr.

The spinning-wing decoy was placed at the discretion of the hunters (including its orientation), as long as it remained within 10–15 m of the hunting blind. In observational trials, the spinning-wing decoy was placed within 10–15 m of the blind at the discretion of the observers. For the control treatment, we removed the spinning-wing decoy. We used

a 'goal-post style' mechanical spinning-wing decoy (Motoduck Enterprises, Woodland, California) that had a rotating oval blade with a fixed rotation speed of 500–750 rpm, length of 61 cm, and maximum width of 18.5 cm. The blade was painted dark brown on one side and white on the other. We used 124 ± 143 traditional decoys during hunting trials that consisted mainly of Mallard (about 75%), Northern Pintail (20%), and American Green-winged Teal (5%) decoys. We used 17 ± 1 Mallard decoys during observational trials. Importantly, we used the same number of decoys for each paired decoy treatment, so ducks were exposed to similar conditions. Our goal was not to compare hunting and observational trials, so the differences in decoy numbers between trial types are not relevant.

During each hunting and observational trial, we recorded each duck flock ($\geq$1 duck) that approached to within 100 m of the hunting blind. For each of these flocks, we recorded species and flock size, and estimated the flock's minimum approach distance (m). We used laser range finders (Bushnell® Yardage Pro 500, Bushnell Corporation, Overland Park, Kansas) to improve our ability to accurately estimate the distances to flocks. From these data, we calculated the proportion of flocks within 100 m that approached to within 45 m of the hunting blind for each species.

STATISTICAL ANALYSES

For all hunting and observational trials, we averaged the minimum approach distance and proportion of flocks taking risk (approaching to $\leq$45 m) for each species ($n = 7$) instead of using each flock ($n = 1099$ for hunting trials and $n = 491$ for observational trials) as the sampling unit, because flocks may not be statistically independent of one another. We excluded mixed flocks from analysis (<1% of observations). Mean minimum approach distances were normally distributed and we normalized the proportion of flocks taking risk using an arcsine square-root transformation.

Phylogeny explains a significant amount of the variation in numerous life-history traits for many species (Stearns 1983, 1984, Felsenstein 1985, Harvey and Pagel 1991), including waterfowl (Arnold 1988, Laurila 1988, Krementz et al. 1997). We corrected for the influence of phylogeny using independent con-

trasts analyses (Felsenstein 1985) as implemented in program PDAP (Garland et al. 1993, 1999, 2001, Garland and Ives 2000). We used the phylogenetic tree by Livezey (1986, 1991, 1997) as modified by Figuerola and Green (2000:fig. 1), although analyses using Johnson's (2000) phylogeny for dabbling ducks (Anatini) produced similar results (differences in R^2 were typically <5%). We conducted our analyses using two sets of arbitrary branch lengths. Pagel's (1992) method sets all internode segments equal to one, but branch tips are constrained to be contemporaneous; Grafen's (1989) method also constrains tips to be contemporaneous, but the depth of each node is set equal to one less than the number of tip species that descend from it (Garland et al. 2001). We used the diagnostics recommended by Garland et al. (1992, 2001) to evaluate the performance of these methods. We detected no significant correlation between the values of the standardized contrasts and their standard deviations in either case. Moreover, the R^2 values from subsequent independent contrasts analyses differed by less than 5% using the two different methods. We present the results of analyses using Pagel's (1992) method here.

Independent contrasts analyses were used to test the strength of associations between indices of risk-taking behavior (i.e., mean minimum approach distance and the proportion of flocks within 100 m that subsequently approached to within 45 m of the hunting blind) and life-history characteristics (i.e., reproductive output, adult female body mass, and adult female annual survival rate). We report R^2 and F-values calculated from the regression through the origin for the independent contrasts (Garland and Ives 2000). Because we used two indices of risk-taking behavior and three indices of life-history characteristics, we controlled for the six statistical comparisons using the sequential Bonferroni correction (Rice 1989). The usefulness of phylogenetic comparative methods has been questioned by some authors (Ricklefs and Starck 1996, Björklund 1997, Price 1997); therefore, we also performed analyses using the original data without the phylogenetic correction. Both statistical approaches resulted in the same patterns, so we present only the analyses using independent contrasts for simplicity. Because flock size can influence risk-taking behavior in birds (Mori et

al. 2001), we repeated the analyses comparing approach behaviors and life-history parameters using the original data after controlling for the effect of average flock size using partial correlation analysis. We also tested whether the body condition of harvested birds influenced approach behaviors among species (excluding Cinnamon Teal due to small sample sizes). We estimated body condition using the residuals from a regression of body mass on the first principal component of structural size (culmen, tarsus, and wing length). We further tested whether age ratios (proportion of juveniles to adults) of harvested ducks influenced approach behaviors among species (excluding Cinnamon Teal due to small sample sizes). Finally, we tested for interactions between the effect of the spinning-wing decoy and reproductive output on both indices of risk-taking behavior using ANCOVA with the original data. We conducted statistical analyses with StatView® version 5.0.1 (SAS Institute 1998), with α = 0.05.

RESULTS

LIFE-HISTORY PARAMETERS

The life-history characteristics of dabbling ducks are summarized in Table 1. Of the seven dabbling ducks considered in this study, American Green-winged Teal are the smallest and Mallards are the largest. Reproductive output is highest in Cinnamon Teal, which produce clutches that weigh 75% of their body mass on average, and lowest in Northern Pintails, which produce clutches that weigh 36% of their body mass on average. Annual survival rates of the adult female dabbling ducks studied were grouped at either low (0.46–0.48) or high values (0.58–0.63). As expected, female body mass, reproductive output, and annual survival rate were all highly correlated (body mass and reproductive output: $r = -0.91$, $n = 7$, $P = 0.003$; body mass and annual survival rate: $r = 0.80$, $n = 7$, $P = 0.03$; reproductive output and annual survival rate: $r = -0.82$, $n = 7$, $P = 0.02$).

RISK-TAKING BEHAVIORS

During the 37 hunting trials, we recorded 1099 dabbling duck flocks approaching to within 100 m of hunters, of which 29% were Mallard, 23% were American Green-winged Teal, 16%

TABLE 1.   Life-history traits of seven congeneric female dabbling ducks. Species are ordered from left to right along the slow–fast life-history gradient (analogous to *K*- and *r*-selection); thus, Northern Pintails are considered to have the slowest life-history strategy (longer-lived and less fecund), whereas Cinnamon Teal are considered to have the fastest life-history strategy (shorter-lived and more fecund).

Trait	Species						
	Northern Pintail	Mallard	American Wigeon	Gadwall	Northern Shoveler	American Green-winged Teal	Cinnamon Teal
Mean clutch size[a]	7.8	9.0	8.5	10.0	9.4	8.6	8.9
Mean egg mass (g)[b]	40.3	49.9	44.1	45.9	39.1	25.2	30.8
Clutch mass (g)[c]	313	449	375	461	368	217	273
Mean adult female body mass (g)[d]	866	1107	767	835	590[e]	308	363[e]
Reproductive output[f]	36%	41%	49%	55%	62%	70%	75%
Annual survival rate[g]	0.61	0.58	0.60	0.63	0.46	0.48	0.46[h]

[a] Data from Bellrose (1976). Sample sizes of nests are: 1276 Northern Pintail; 5170 Mallard; 179 American Wigeon; 2545 Gadwall; 585 Northern Shoveler; 91 American Green-winged Teal; 1368 Cinnamon Teal.

[b] Data from Rohwer (1988).

[c] Clutch mass (g) = mean clutch size · mean egg mass (g).

[d] Data from Bellrose (1976) except where noted otherwise. Sample sizes of birds are: 166 Northern Pintail; 1417 Mallard; 68 American Wigeon; 45 Gadwall; 71 Northern Shoveler; 79 American Green-winged Teal; 19 Cinnamon Teal.

[e] Data from Dunning (1993) because of larger sample sizes than Bellrose (1976).

[f] Index of reproductive output = mean clutch mass (g) / mean female mass (g); following Forbes et al. (1994).

[g] Average annual adult female survival rate reported by Krementz et al. (1997) for North America.

[h] Data from Gammonley (1996) because Krementz et al. (1997) did not report an annual survival rate estimate for this species.

were Northern Shoveler, 13% were American Wigeon, 10% were Northern Pintail, 6% were Gadwall, and 3% were Cinnamon Teal (Table 2). During 13 observational trials, we recorded 491 dabbling duck flocks, of which 49% were Mallard, 13% were American Green-winged Teal, 10% were Gadwall, 10% were Northern Shoveler, 9% were Northern Pintail, 8% were American Wigeon, and 2% were Cinnamon Teal (Table 2). In both hunting and observational trials, Cinnamon Teal generally took the greatest amount of risk: this species approached hunting sites most closely and had the highest percentage of flocks approach to within 45 m of the hunting blind. Northern Pintails took the least amount of risk, remaining the farthest from the hunting site and having the lowest percentage of flocks approach to within 45 m of the hunting blind (Table 2).

RISK-TAKING BEHAVIOR AND LIFE HISTORY

During both hunting and observational trials, approach behaviors of dabbling ducks were strongly correlated with life-history characteristics (Table 3). Mean minimum approach distance was negatively correlated with reproductive output during each decoy treatment and trial type (Fig. 2a, c). Thus, smaller-bodied species with higher fecundity (e.g., Cinnamon Teal) approached decoys more closely than did larger-bodied species with lower fecundity (e.g., Northern Pintail). The percentage of flocks approaching to ≤45 m was positively correlated with reproductive output during each decoy treatment and trial type (Fig. 2b, d). Smaller-bodied species with higher fecundity more often approached decoys to within shotgun range than did larger-bodied species with lower fecundity. We found similar patterns of approach behavior when we used other measures of life history (i.e., adult female body mass and annual adult female survival rate; Table 3), but approach behavior tended to be more strongly correlated with reproductive output.

Minimum approach distance declined with increasing flock size in one of the four decoy treatments (hunting trials with traditional decoys: $r = -0.80$, $n = 7$, $P = 0.03$), but not during the other decoy treatments (hunting trials with spinning-wing decoys: $r = -0.72$, $n = 7$, $P = 0.07$; observational trials with

TABLE 2.   Behavior (mean ± SE) of dabbling ducks approaching landing sites during hunting trials (16 October 1999 to 23 January 2000) and posthunting season observational trials (27 January–21 February 2000) in the Central Valley of California, split by whether traditional, stationary decoys were used alone or used in combination with a spinning-wing decoy. Number of flocks = the number of flocks approaching to within 100 m of the landing site; minimum approach distance = the average minimum approach distance by flocks within 100 m; flocks taking risk = the percentage of flocks within 100 m that approached to within 45 m of the hunting blind (i.e., to within shooting range); and flock size = the mean size of flocks that approached to within 100 m.

Trial Decoy treatment Behavior	Species						
	Northern Pintail	Mallard	American Wigeon	Gadwall	Northern Shoveler	American Green-winged Teal	Cinnamon Teal
Hunting trials							
Traditional decoys only							
Number of flocks	49	124	44	27	77	112	11
Minimum approach distance (m)	60 ± 3	54 ± 2	55 ± 3	54 ± 4	48 ± 2	41 ± 2	34 ± 5
Flocks taking risk	39% ± 7%	42% ± 4%	43% ± 8%	41% ± 10%	64% ± 6%	71% ± 4%	91% ± 9%
Flock size	2.5 ± 0.2	2.7 ± 0.5	2.2 ± 0.3	1.9 ± 0.2	2.8 ± 0.3	2.7 ± 0.3	4.2 ± 1.3
Spinning-wing and traditional decoys							
Number of flocks	56	195	101	39	98	144	22
Minimum approach distance (m)	55 ± 3	53 ± 2	50 ± 2	48 ± 4	45 ± 2	39 ± 2	40 ± 3
Flocks taking risk	43% ± 7%	48% ± 4%	56% ± 5%	59% ± 8%	64% ± 5%	73% ± 4%	86% ± 7%
Flock size	2.6 ± 0.3	2.5 ± 0.2	2.7 ± 0.2	2.6 ± 0.3	2.9 ± 0.3	3.7 ± 0.5	6.1 ± 1.7
Posthunting season trials							
Traditional decoys only							
Number of flocks	13	53	11	18	9	19	1
Minimum approach distance (m)	64 ± 7	57 ± 3	56 ± 8	58 ± 5	43 ± 8	31 ± 3	35.0
Flocks taking risk	31% ± 13%	34% ± 7%	46% ± 15%	28% ± 11%	67% ± 16%	95% ± 5%	100.0%
Flock size	2.9 ± 0.6	2.2 ± 0.2	2.7 ± 0.6	2.0 ± 0.2	2.4 ± 0.6	1.8 ± 0.3	3.0
Spinning-wing and traditional decoys							
Number of flocks	32	187	27	31	38	43	9
Minimum approach distance (m)	49 ± 3	49 ± 2	41 ± 4	38 ± 4	37 ± 3	28 ± 3	26 ± 4
Flocks taking risk	56% ± 9%	56% ± 4%	74% ± 8%	77% ± 8%	82% ± 6%	88% ± 5%	89% ± 11%
Flock size	3.8 ± 0.6	2.0 ± 0.1	2.7 ± 0.3	2.6 ± 0.3	2.7 ± 0.3	3.1 ± 0.9	2.2 ± 0.3

TABLE 3. Relationships between approach behaviors (i.e., minimum approach distance and the proportion of flocks approaching to within 45 m) and life-history characteristics (i.e., reproductive output, adult female body mass, and annual adult female survival rate) of seven congeneric dabbling duck species in the Central Valley of California. Separate phylogenetically independent contrasts analyses were run for each combination of trial type (i.e., hunting trials [16 October 1999 to 23 January 2000] or posthunting season observational trials [27 January–21 February 2000]) and decoy treatment (i.e., traditional, stationary decoys used alone or used in combination with a spinning-wing decoy). Statistically significant P values (alpha = 0.05) after sequential Bonferroni correction are noted with a single asterisk; highly significant P values (alpha = 0.01) are indicated with two asterisks.

Trial Decoy treatment Behavior	Species sample size	Reproductive output			Body mass			Survival rate		
		R^2	F	P	R^2	F	P	R^2	F	P
Hunting trials										
Traditional decoys only										
Minimum approach distance	7	0.89	39.9	0.002*	0.79	18.9	0.007*	0.67	10.2	0.02*
Proportion of flocks taking risk	7	0.85	29.2	0.003*	0.85	28.2	0.003*	0.72	13.0	0.02*
Spinning-wing and traditional decoys										
Minimum approach distance	7	0.99	576.2	< 0.001**	0.88	37.4	0.002**	0.77	16.5	0.01*
Proportion of flocks taking risk	7	0.94	83.6	< 0.001**	0.84	27.1	0.003**	0.66	9.5	0.03*
Posthunting season trials										
Traditional decoys only										
Minimum approach distance	7	0.90	46.2	0.001**	0.86	30.5	0.003**	0.87	33.2	0.002**
Proportion of flocks taking risk	7	0.84	26.3	0.004**	0.90	46.7	0.001**	0.82	22.3	0.005**
Spinning-wing and traditional decoys										
Minimum approach distance	7	0.98	225.2	< 0.001**	0.90	46.3	0.001**	0.68	10.5	0.02*
Proportion of flocks taking risk	7	0.96	127.6	< 0.001**	0.90	44.4	0.001**	0.74	14.5	0.01*

traditional decoys: $r = 0.15$, $n = 7$, $P = 0.76$; observational trials with spinning-wing decoys: $r = 0.01$, $n = 7$, $P = 0.99$). Because flock size might have influenced approach behavior, we repeated the analyses between approach behaviors and life-history characteristics after controlling for the effect of flock size using partial correlation analysis. Approach behaviors remained correlated with indices of life history (Table 4). Body condition might also have influenced approach behavior; however, the average body condition of harvested birds among species was not correlated with either index of risk-taking behavior during hunting or observational trials (all $R^2 < 0.25$, all $P > 0.35$, $n = 6$). Finally, differential age ratios among species could influence approach behavior irrespective of life-history strategy; however, the age ratio of harvested ducks ($n = 185$) also was not correlated with indices of

risk-taking behavior (all $R^2 < 0.29$, all $P > 0.27$, $n = 6$).

MANIPULATING THE ATTRACTIVENESS OF THE STUDY SITE

Approach behavior of dabbling ducks was strongly influenced by the presence of a spinning-wing decoy during observational trials, but not during hunting trials. During hunting trials, we detected no significant interaction between reproductive output and presence of the spinning-wing decoy on the mean minimum approach distance (ANCOVA: $F_{1,10} = 2.4$, $P = 0.16$). After dropping the nonsignificant interaction term, reproductive output (ANCOVA: $F_{1,11} = 83.8$, $P < 0.001$), but not presence of the spinning-wing decoy (ANCOVA: $F_{1,11} = 2.7$, $P = 0.13$), influenced the mean minimum distance to which ducks approached the hunting blind. Similarly, after
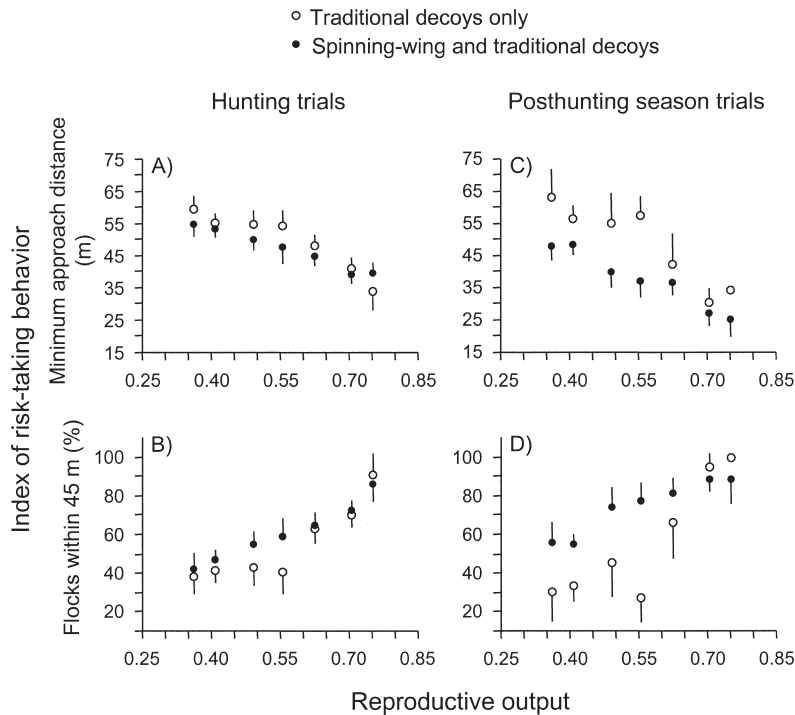
FIGURE 2.   The risk-taking behaviors of seven congeneric dabbling ducks were strongly correlated with their reproductive output (a life-history trait calculated by dividing the mean clutch mass [g] by the mean female mass [g] for each species), both when the predation risk was high (on active hunts conducted during the 1999–2000 waterfowl hunting season) and when the predation risk was low (posthunting season trials) in the Central Valley of California, USA. The relationships between risk-taking behavior and life history remained robust when we experimentally manipulated the attractiveness of study sites by using a spinning-wing decoy. Risk-taking behavior was indexed using a flock's minimum approach distance (m) and the proportion of flocks within 100 m that approached to within 45 m (shooting range). Filled circles indicate data collected when the spinning-wing decoy was used in combination with traditional decoys and calls, and unfilled circles indicate data collected when only traditional decoys and calls were used (mean ± SE; SE are displayed either above or below the mean to improve clarity). For all panels, species from left to right are: Northern Pintail, Mallard, American Wigeon, Gadwall, Northern Shoveler, American Green-winged Teal, and Cinnamon Teal. Sample sizes (number of flocks) from left to right are: (a–b) filled circles, 56, 195, 101, 39, 98, 144, 22; unfilled circles, 49, 124, 44, 27, 77, 112, 11; (c–d) filled circles, 32, 187, 27, 31, 38, 43, 9; unfilled circles, 13, 53, 11, 18, 9, 19, 1.

dropping the nonsignificant interaction term (ANCOVA: $F_{1,10} = 0.7$, $P = 0.44$), we detected a significant effect of reproductive output (ANCOVA: $F_{1,11} = 53.5$, $P < 0.001$), but not of the spinning-wing decoy (ANCOVA: $F_{1,11} = 1.4$, $P = 0.27$), on the proportion of flocks within 100 m that approached to within 45 m of the hunting blind.

In contrast, during observational trials we detected a significant effect of both reproductive output (ANCOVA: $F_{1,11} = 77.7$, $P < 0.001$) and the presence of the spinning-wing decoy (ANCOVA: $F_{1,11} = 25.5$, $P < 0.001$) on

mean minimum approach distance, when the nonsignificant interaction term (ANCOVA: $F_{1,10} = 1.6$, $P = 0.23$) was excluded. When we considered the proportion of flocks within 100 m that approached to within 45 m, we detected a significant interaction between reproductive output and use of the spinning-wing decoy (ANCOVA, decoy: $F_{1,10} = 7.7$, $P = 0.02$; reproductive output: $F_{1,10} = 37.7$, $P < 0.001$; decoy × reproductive output: $F_{1,10} = 5.8$, $P = 0.04$). Larger-bodied species with lower fecundity took relatively more risk when the spinning-wing decoy was used than when only

TABLE 4. Partial correlation coefficients after controlling for the effect of flock size (species average) on the relationships between approach behaviors (i.e., minimum approach distance and the proportion of flocks approaching to within 45 m) and life-history characteristics (i.e., reproductive output, adult female body mass, and annual adult female survival rate) of seven congeneric dabbling duck species in the Central Valley of California. Separate analyses were run for each combination of trial type (i.e., hunting trials [16 October 1999 to 23 January 2000] or posthunting season observational trials [27 January–21 February 2000]) and decoy treatment (i.e., traditional, stationary decoys used alone or used in combination with a spinning-wing decoy). Statistically significant P values (alpha = 0.05) after sequential Bonferroni correction are noted with a single asterisk; highly significant P values (alpha = 0.01) are indicated with two asterisks.

Trial
  Decoy treatment
    Behavior
	Species sample size	Reproductive output
		r
			Body mass
			r
				Survival rate
				r

Hunting trials				
Traditional decoys only				
Minimum approach distance	7	−0.97**	0.84	0.68
Proportion of flocks taking risk	7	0.98**	−0.94*	−0.80
Spinning-wing and traditional decoys				
Minimum approach distance	7	−0.98**	0.85	0.65
Proportion of flocks taking risk	7	0.99**	−0.75	−0.59
Posthunting season trials				
Traditional decoys only				
Minimum approach distance	7	−0.93*	0.94*	0.91*
Proportion of flocks taking risk	7	0.76	−0.82	−0.68
Spinning-wing and traditional decoys				
Minimum approach distance	7	−0.99**	0.97**	0.74
Proportion of flocks taking risk	7	0.62	−0.55	−0.32

traditional decoys were used, whereas smaller-bodied species with higher fecundity took a similar amount of risk when the spinning wing decoy was used (Fig. 2d).

DISCUSSION

The degree to which dabbling ducks were willing to approach a landing site with hunting decoys was strongly correlated with life-history parameters. Species characterized by a faster life history (i.e., higher fecundity and shorter lifespan) approached decoys more closely than species with a slower life-history strategy (i.e., lower fecundity and longer lifespan). These patterns remained robust during hunting trials, when predation risk was high, and during posthunting season observational trials, when predation risk was low. Moreover, although we were able to reduce risk-averseness, we were unable to override the influence of life history on the approach behavior of dabbling ducks by experimentally manipulating the attractiveness of the site using a spinning-wing decoy. Thus, life history appeared to influence the risk-taking

behavior of dabbling ducks, consistent with the predictions of Figure 1b (during hunting trials) and Figure 1c (during observational trials).

Several alternative hypotheses could also explain these patterns. First, hunter behavior could have influenced our measures of risk-taking behavior, resulting in a spurious correlation with life-history characteristics. For example, hunters may have restricted the minimum approach distances of flocks by shooting at approaching birds. Hunters also may have selected larger-bodied species, shot at these species from farther distances, and thereby disproportionately limited the minimum approach distances of larger birds. However, two lines of evidence indicate that the observed relationships between life-history characteristics and risk-taking behaviors are not an artifact of our methods. First, life-history characteristics were positively correlated with minimum approach distance during observational trials conducted after the hunting season when no shooting occurred; hunter behavior could not have influenced the minimum approach dis-

tance of waterfowl flocks in these trials. Second, we examined an additional index of risk-taking behavior that is insensitive to hunter behavior (i.e., the proportion of flocks within 100 m that approached to within 45 m), and found that life-history characteristics were still correlated with approach behavior.

A second alternative hypothesis is that, if hunters consistently selected larger-bodied species for harvest over time, larger-bodied species may have learned to avoid hunting sites more than smaller-bodied species. If this were the case, risk-averseness by larger-bodied species may be a consequence of hunter preference, rather than life history. Band recovery rates of North American waterfowl tend to increase with body size (Botero and Rusch 1988), thus we cannot exclude this as an alternative explanation. However, band recovery rates are a function not only of harvest rates, but also of survival and reporting rates. Because body size and survival rate are correlated (due to life history), it is difficult to determine whether high reporting rates for large-bodied species is due to hunter preference based on size, or the higher survival rates of those species providing hunters with more opportunities to harvest long-lived individuals.

A third hypothesis is that approach distance does not indicate risk-taking behavior per se, but instead is an index of some other factor such as the degree of sociality, flock size, age ratios, or body condition among species. For example, the observed relationship between approach distance and life history may have resulted if species with faster life histories (e.g., teal) are also more social than species with slower life histories (e.g., Northern Pintails) and therefore more inclined to approach conspecifics or decoys. However, all of the species that we studied are highly gregarious during the winter, and both Mallards (slow life history) and Green-winged Teal (fast life history) select sites with conspecifics more often than unoccupied sites (Pöysä 1987, Pöysä et al. 1998). Alternatively, differences in flock size among species might account for the observed relationship between approach distance and life history if, for example, species with faster life histories fly in larger flocks than species with slower life histories. However, when we used partial correlation analysis to control for the effect of flock size on approach distance, we found that

approach distance was still highly correlated with life history. Another possibility is that species with faster life histories have higher age ratios of juveniles to adults during winter than species with slower life histories, and therefore that species with faster life histories approach more closely because they are represented by younger and more naive birds. We found no evidence of this; age ratios of harvested ducks were not correlated with approach behaviors. A final possibility is that smaller-bodied ducks may be more energetically challenged than larger-bodied species (Nagy 2005), so that approach distance indicates energetic state rather than risk-taking behavior. However, the body condition of harvested birds was not correlated with either index of risk-taking behavior. Therefore, differences in flock size, sociality, age ratios, or body condition among species do not explain the observed relationship between approach distance and life history.

Few studies have directly examined the influence of life history on risk-taking behaviors, but of those that have, all have found that risk-taking behavior by adults in defense of their offspring is related to life-history strategy. For example, Forbes et al. (1994) showed that both nest desertion rates and the minimum distance that females allowed a potential predator (i.e., an observer) to approach before flushing from their nests were negatively correlated with annual mortality rates. Females of species with high annual mortality rates, such as Blue-winged Teal (*A. discors*) and Northern Shovelers, took greater risks and had lower rates of nest desertion than females of species with lower annual mortality rates, such as Mallards. Similarly, Gunness et al. (2001) found that female Blue-winged Teal allowed observers to approach their nests more closely than did Gadwalls or Mallards. White-breasted Nuthatch parents (*Sitta carolinensis*) took greater risks than Red-breasted Nuthatch parents (*S. canadensis*) when exposed to a predator and White-breasted Nuthatches also have a faster life-history strategy (lower survival and more fecund; Ghalambor and Martin 2000). Ghalambor and Martin (2001) further found that passerines in the Northern Hemisphere, which have a lower probability of adult survival and larger clutch sizes than passerines in the Southern Hemisphere, tolerated greater predation risk to themselves, but not to their

offspring, than Southern Hemisphere parents. Thus, shorter-lived and more fecund species generally take greater risks when exposed to predation than longer-lived and less fecund species, probably because the fitness value of current offspring is high for species with fast life-history strategies compared to the prospects for future survival and reproduction. We found that risk-taking behavior is correlated with life history during the nonbreeding season as well, a result that has not been reported previously. Our results are also unique in that we were able to use a real predation threat (human predation), whereas other studies have, of necessity, simulated predation risk (Forbes et al. 1994, Ghalambor and Martin 2000).

Our results suggest that life history may predispose waterfowl species to differential harvest, such that species with faster life-history strategies may be more susceptible to harvest than species with slower life histories. In addition, the effect of novel decoy techniques such as spinning-wing decoys (Ackerman et al. 2006) and electronic calls (Olsen and Afton 2000) may differ depending on the life history of a species. For example, we detected an interaction between reproductive output and the decoy treatment on one measure of risk-taking: the proportion of flocks within 100 m that approached to within 45 m of the hunting blind during posthunting season trials. Larger-bodied species with lower fecundity tended to take relatively more risk when the spinning-wing decoy was used than when only traditional decoys were used, whereas smaller-bodied species with higher fecundity tended to take a relatively equivalent amount of risk during both decoy treatments. Similarly, in a larger study at six sites in North America, we found that the vulnerability of dabbling ducks to spinning-wing decoys increased with annual survival rates, indicating that species with slower life histories may be more negatively affected by novel decoy techniques than those with faster life histories (Ackerman et al. 2006). Currently, biologists setting regulations using the Adaptive Harvest Management process are exploring ways to incorporate the life-history traits of different species into harvest regulations (Multiple-Stock Adaptive Harvest Management: Johnson et al. 2002, U.S. Fish and Wildlife Service 2003). Our results suggest that life history may be an important component

influencing the susceptibility of waterfowl to harvest and that managers should take this into account when developing modified harvest models.

ACKNOWLEDGMENTS

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