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Authors: Dufour, Kevin W., and Ankney, C. Davison

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Hunting mortality of mallards *Anas platyrhynchos* in relation to time of day, flocking behaviour, and individual condition

Kevin W. Dufour & C. Davison Ankney

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Diurnal variation in the number of mallards *Anas platyrhynchos* shot by hunters at Long Point, Ontario, was assessed during the 1989 hunting season to determine peak periods of harvest and to test the prediction that ducks shot during non-peak periods would be in poor relative condition. In addition, attempts were made to determine whether lone mallards are disproportionately vulnerable to hunting and whether ducks shot as singles are in poor condition relative to those shot from flocks. Diurnal variation in size of the harvest was pronounced, with peak harvest occurring during the first third of the day. Relatively few ducks were shot at mid-day, suggesting that mallards were largely inactive at this time. Analysis of abdominal fat masses, however, revealed no relationship between individual condition and time shot. Single mallards were apparently more vulnerable to hunting than were those occurring in flocks, as the hunter-shot sample contained a high proportion of lone birds relative to an expected frequency based on observational data. However, no evidence of a relationship between individual condition and status (i.e. alone vs. in a flock) at the time of harvest was found. Our results, in conjunction with previous work, suggest that flocking behaviour may be a general component of hunting mortality in waterfowl and furthermore that increased vulnerability of lone birds can occur independently of variation in individual condition.

Key words: condition, flocking behaviour, harvest, hunting mortality, mallard

Kevin W. Dufour* & C. Davison Ankney, Department of Zoology, University of Western Ontario, London, Ontario, N6A 5B7, Canada

* Present address: Department of Biology, Carleton University, 1125 Colonel By Dr., Ottawa, Ontario, K1S 5B6, Canada

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Biologists have long recognised that certain segments of exploited waterfowl populations may be more susceptible to hunting mortality than others. It is well established, for example, that juvenile waterfowl are more vulnerable to hunting than are adults (e.g. Geis 1959, Anderson 1975, Krementz et al. 1987, Nichols et al. 1990, Caithness et al. 1991). Similarly, male ducks typically are more vulnerable than their female counterparts (e.g. Anderson 1975, Reinecker 1976, Blohm et al. 1987, Nichols et al. 1990), although in canvasbacks *Aythya valisineria* and redheads *A. americana* the opposite may be true (Olson 1964, Benson & Degraff 1968). Additional factors that appear to influence hunting vulnerability include plumage brightness

(Metz & Ankney 1991), disease (e.g. lead poisoning, Bellrose 1959), and flocking behaviour (Olson 1964, Bain 1980). Identification of such patterns has been central to the development of waterfowl harvest management in North America and elsewhere.

Recent studies have focused on the relationship between vulnerability to hunting and physiological condition, where condition is broadly defined as the nutritional status of an individual relative to its requirements at a particular time (Weatherhead & Ankney 1984), but generally refers to energy storage in the form of fat (see Johnson et al. 1985). Weatherhead & Ankney (1984) proposed that because individuals in poor condition have

greater need for food, they should be more readily attracted to hunters' decoys, and consequently more vulnerable to hunting, than individuals in superior condition. This prediction has since been supported by band-recovery data on mallards *Anas platyrhynchos* (Hepp et al. 1986, Dufour et al. 1993a), by radio-telemetry data on American black ducks *A. rubripes* (Conroy et al. 1989), and by comparisons between ducks shot by hunters using decoys and those collected randomly from the same population (Greenwood et al. 1986, Reinecke & Shaiffer 1988, Heitmeyer et al. 1993, although see Sheeley & Smith 1989).

A consistent relationship between condition and vulnerability to hunting has implications for management. For instance, Conroy et al. (1989) suggested that prudent harvest management might be directed towards particularly vulnerable segments of the population (i.e. birds in poor condition). However, such a strategy requires knowledge of how birds in good and poor condition differ in their use of habitats and/or temporal patterns of activity. Unfortunately, waterfowl studies relating condition to habitat use are few (Bain 1980, Nichols & Haramis 1980, Dufour et al. 1993b) and there are virtually no data on how condition influences diurnal patterns of movement. The primary aim of our study was to quantify diurnal variation in the condition of mallards shot by hunters at Long Point, Ontario, during the 1989 hunting season.

Mallards and other duck species staging at Long Point exhibit definite diurnal patterns of activity. Robilliard (1988) interviewed hunters and determined that almost 60% of the mallard harvest at Long Point occurred during the first third of the day, presumably because ducks were most active in feeding flights at that time. Relatively few birds were shot at mid-day, as was also true for redheads and lesser scaup *Aythya affinis*, the other species that she studied. These results are consistent with observations that staging and wintering ducks often exhibit peak periods of movement associated with dawn and, to a lesser extent, dusk (e.g. Winner 1959, Thornburg 1973, Baldassarre & Bolen 1984, Miller 1985). Nevertheless, some ducks are shot during non-peak periods, and for several reasons, we predicted that these individuals might be in relatively poor condition. First, ducks in poor condition are likely to be inferior foragers and therefore might be forced to allocate more of their daily time budget to food finding. Alternatively, ducks in poor condition are likely to be socially subordinate (Patterson 1977, Heitmeyer 1988) and may consequently suffer reduced access to preferred feeding areas (Patterson 1977, Nichols & Haramis 1980, Jorde et al. 1983, Paulus 1983). In either case, individuals in poor condition are expected to spend a greater part of the day flying in search of food. Thus, our specific objectives were (1) to determine the peak periods of harvest for mallards shot at Long Point, and (2) to

test the prediction that individuals shot during non-peak periods are in relatively poor condition.

A secondary aim of our study was to investigate the relationships between condition, hunting vulnerability, and flocking behaviour. Research on canvasbacks (Olson 1964, Bain 1980) and on redheads (Bain 1980) has shown that individuals occurring alone or in small flocks may be more vulnerable to hunting than individuals occurring in large flocks. Bain (1980) further provided evidence that this pattern might be related to individual condition. He found that, among hunter-shot birds, those shot as singles weighed less and had lower abdominal fat masses than did those shot from flocks. While these results suggest that condition, flocking behaviour, and hunting vulnerability are inter-related, causality has not yet been established. Furthermore, the extent to which we can generalise these results to other species is unknown. Thus, our secondary objectives were (1) to determine whether single mallards are particularly vulnerable to hunting, and (2) to test the prediction that mallards shot as singles are in poor condition relative to those shot from flocks.

Methods

Our study was conducted at the Long Point Waterfowl Management Unit (WMU) at Long Point, Ontario (42° 38'N, 80° 24'W), where hunters are legally required to report with their daily kill to a central check station. In 1989, hunting at the WMU occurred 4 days/week from 25 September to 2 December, effectively providing 40 days of opportunity to collect data on hunter-shot ducks. Within limits imposed by the ability of hunters to recall certain information (see below), we endeavoured to collect data on all mallards brought to the WMU check station on 39 of the 40 available hunting days. Legal shooting occurred between half an hour before sunrise and half an hour after sunset.

Hunters contributed by providing information on circumstances surrounding the kill and by allowing examination and dissection of their ducks. Consenting hunters were asked to estimate (to the nearest half hour) the time at which a particular duck was shot and whether it was shot as a single or from a flock (≥ 2 ducks). If the hunter hesitated in providing an answer or was unable to recall this information, or if there was potential for confusion between individual ducks (e.g. 2 ducks of like plumage shot by the same hunter at different times of the day), no further information was recorded. Otherwise, we classified each duck according to sex and age and dissected the carcass to remove the abdominal fat deposit (see below). Sex was determined using plumage (Carney 1964) and cloacal characters (Hochbaum 1942). Juveniles (i.e. birds in their first year) were distinguished from adults by the presence of a bursa of Fabricius (Larson & Taber 1980).

Male age was confirmed by examination of the penis (Hochbaum 1942).

We used the amount of fat deposited in the lower omentum (hereafter called abdominal fat) as our index of condition. We chose abdominal fat because it is easily obtained and because carcass analyses of mallards (Whyte & Bolen 1984, Hanson 1987) and of other duck species (Bailey 1979, Wishart 1979, Chappell & Titman 1983, Hohman & Taylor 1986, Miller 1989) have consistently shown abdominal fat to be an excellent predictor of total body lipids (all correlations > 0.9). In addition, variation in abdominal fat is generally unrelated to variation in structural size (Whyte & Bolen 1984, Hanson 1987, Miller 1989). For each duck included in the study, all abdominal fat (including that adhering to the gizzard) was removed with forceps and weighed to the nearest 0.1 g using a Mettler P1210 electronic balance.

On 19 of the 39 days for which we had data on hunter-shot ducks, we also collected observational data to determine the relative frequencies of lone mallards and mallard flocks in the population at large. All observations were conducted between sunrise and one and a half hours after sunrise (i.e. during the first two hours of legal hunting) using a spotting scope mounted on an elevated platform overlooking the WMU marsh. At the beginning of each daily session, we positioned the spotting scope to observe all flying waterfowl in an arbitrarily selected area of the WMU. We then scored the total number of lone mallards and mallard flocks observed moving through the field of view over a 1-hour period. We varied the position of the spotting scope (and hence the area of the WMU observed) from one day of observation to the next.

Data Analysis

Analysis of frequency data (i.e. harvest) required that we partition samples into discrete diurnal and seasonal periods. Thus, for instance, to accommodate changing day length, we divided each day into nine diurnal periods of equal duration. To assess seasonal effects, we divided the hunting season into early (25 September - 18 October), middle (19 October - 10 November), and late (11 November - 2 December) seasonal periods so that each period included 13 hunting days. To evaluate statistically diurnal variation in the number of mallards shot, and to determine whether diurnal patterns persisted throughout the hunting season, we used replicated goodness-of-fit tests (Sokal & Rohlf 1981:721-731), specifying diurnal period as the class variable and treating seasonal periods as "replicate" samples. A similar approach was used to determine whether diurnal patterns of harvest varied among age/sex classes.

Analysis of condition relative to diurnal period and flocking behaviour required that we first consider other sources of variation in abdominal fat. Thus, we deter-

mined the independent and interactive effects of date, sex, and age using analysis of covariance (ANCOVA, MGLH procedure, SYSTAT, Wilkinson 1989), specifying abdominal fat as the dependent variable and treating date as a continuous predictor (i.e. the covariate). Abdominal fat levels were first ln-transformed because scatter plots had revealed substantial heteroscedasticity (variance in abdominal fat tended to increase as the season progressed). An initial model revealed a significant age*date interaction ($F = 15.86, P < 0.001$), indicating that the relationship between fat and date differed between the two recognizable age classes. Specifically, both juvenile and adult mallards gained fat as the season progressed, but adults did so at a greater rate (Table 1). ANCOVA models developed separately by age revealed no differences between the sexes in either the fat versus date relationship (sex*date interaction: juveniles, $F = 1.29, P = 0.256$; adults, $F = 1.50, P = 0.222$) or in the absolute amount of fat stored at a given point in the season (sex effect, interactions removed: juveniles, $F = 0.01, P = 0.918$; adults, $F = 2.48, P = 0.116$).

To control seasonal effects in subsequent analyses, we computed adjusted fat levels based on residuals from simple linear regressions describing the relationship between abdominal fat and date (see Sokal & Rohlf 1981:491-496). For reasons outlined above, regressions were conducted separately by age (but with the sexes pooled) and an adjusted fat value (m_{adj}) was computed for each individual according to the equation

$$m_{adj} = (m_{obs} - m_{exp}) + \bar{m}_{obs}$$

where m_{obs} is the observed ln-transformed mass of abdominal fat, m_{exp} is the expected value computed from the regression equation, and \bar{m}_{obs} is the mean observed value of all individuals included in the model. Thus, condition hereafter refers to mass of abdominal fat adjusted to a common mean date. Because fat levels of juveniles and adults were adjusted using different regression equations, all subsequent tests were conducted separately by age.

We used factorial analysis of variance (ANOVA, MGLH procedure, SYSTAT, Wilkinson 1989) to assess

Table 1. Simple linear regression models describing the relation between abdominal fat (g, ln[x+1]-transformed) and date for mallards shot by hunters at Long Point, Ontario, September-December 1989. All models significant at $P \leq 0.001$.

Age	Sex	n	Intercept	Slope	r ²
Juv	M	220	1.25	0.024	0.27
	F	183	1.41	0.019	0.18
Ad	M	181	1.08	0.032	0.44
	F	109	0.74	0.038	0.46

the independent and interactive effects of sex and diurnal period on individual condition. An analogous procedure was used to evaluate condition relative to sex and flock status. Each initial ANOVA model included a 2-way interaction. If the interaction was not significant ($P > 0.05$), it was removed and a new reduced model (reported herein) was developed.

Results

Collectively, hunters provided information on both time shot and flock status for 655 mallards. For an additional 38 birds, we obtained information on flock status only (i.e. hunters were unable to recall with sufficient precision the times at which these birds were shot). Thus, sam-

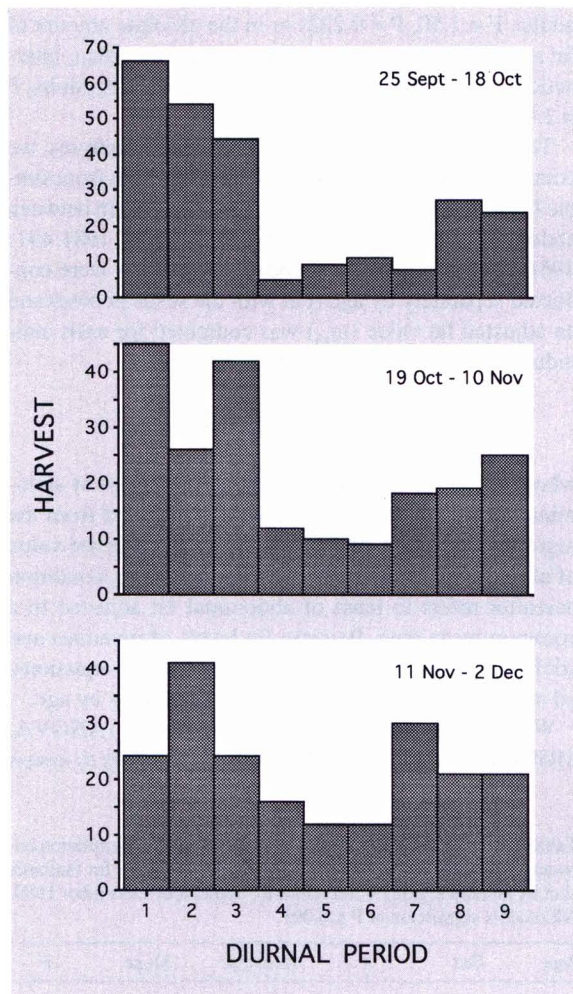


Figure 1. Diurnal pattern of harvest for mallards shot at Long Point, Ontario, during the 1989 hunting season. Diurnal periods are of equal duration and collectively include all legal shooting times (i.e. from half an hour before sunrise to half an hour after sunset). Data from days in the same seasonal period are combined.

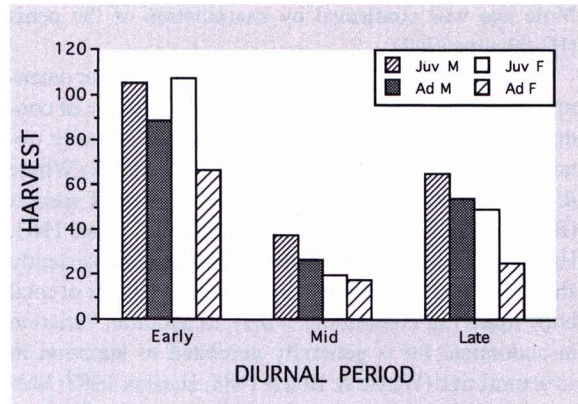


Figure 2. Diurnal variation in the size of the mallard kill by age and sex. Diurnal periods are of equal duration and collectively include all legal shooting times (i.e. from half an hour before sunrise to half an hour after sunset).

ple sizes vary among analyses. Most birds (94%) included in the study were reported to have been shot over decoys.

Time of day

As predicted, the number of mallards killed varied substantially according to time of day. In each of the three seasonal periods examined, peak harvest occurred during the first third of the day, relatively few ducks were shot at mid-day, and a second, lesser peak was observed near the end of the day (Fig. 1). Despite this qualitative agreement, however, heterogeneity among seasonal periods was significant ($G_H = 54.12$, $df = 16$, $P < 0.001$), suggesting subtle seasonal differences in distribution of the harvest *within* each of the three broad temporal categories. Thus, we reclassified individuals according to whether they were shot during the first third of the day, at mid-day, or during the final third of the day, and combined data from the three seasonal periods for subsequent analysis. An analysis of harvest based on this revised classification revealed highly significant differences among diurnal periods (Fig. 2; $G_p = 172.79$, $df = 2$, $P < 0.001$) and indicated that the diurnal pattern was consistent among the recognisable age/sex classes (Fig. 2; $G_H = 8.58$, $df = 6$, $P > 0.1$).

Because most of the mallard harvest occurred either early or late in the day, our prediction was that mallards shot at mid-day would be in relatively poor condition. This prediction was not supported. Although juveniles shot at mid-day tended to be in poor condition relative to those shot at other times (Table 2), the same was not true of adults (Table 2). In neither case did differences approach statistical significance, despite our large sample sizes (Table 3). Thus, we found no evidence to suggest

Table 2. Condition measured as mass of abdominal fat (g) adjusted to a common mean date (see text) of hunter-shot mallards classified according to age, sex and the time of day at which they were shot. Diurnal periods are as follows: early = first third of the day, mid = middle third, late = final third.

Age	Sex	Diurnal period	n	Condition	
				\bar{x}	SD
Juv	M	Early	105	10.43	0.77
		Mid	37	10.21	0.90
		Late	65	10.41	0.82
	F	Early	107	10.41	0.79
		Mid	19	10.29	0.81
		Late	49	10.42	0.94
Ad	M	Early	88	12.36	0.66
		Mid	26	12.27	0.53
		Late	54	12.23	0.94
	F	Early	66	12.06	0.77
		Mid	14	12.29	0.84
		Late	25	12.35	0.71

that individuals shot during non-peak periods suffer this fate as a consequence of poor condition.

Flocking behaviour

To determine whether single mallards were overrepresented in the kill, we compared the proportion of mallards reportedly shot as singles with an expected proportion based on our observational data. For each day of observation, the expected proportion (p_{exp}) was computed according to

$$p_{exp} = n_s / (n_s + n_f)$$

where n_s and n_f represent the number of single mallards and mallard flocks observed, respectively. Because our observations were limited to the first few hours of legal hunting (see page 91), we used only those hunter-killed ducks reported to have been shot during the first third of

Table 3. Two-way analysis of variance evaluating effects of diurnal period and sex on the condition (see Table 2) of hunter-shot juvenile and adult mallards. Interactions were not significant ($P > 0.05$) and were therefore removed from each model.

Age	Model		Source	df	F	P
	n	r^2				
Juv	382	0.01	Period	2	1.186	0.306
			Sex	1	0.000	0.999
Ad	273	0.01	Period	2	0.058	0.943
			Sex	1	2.144	0.144

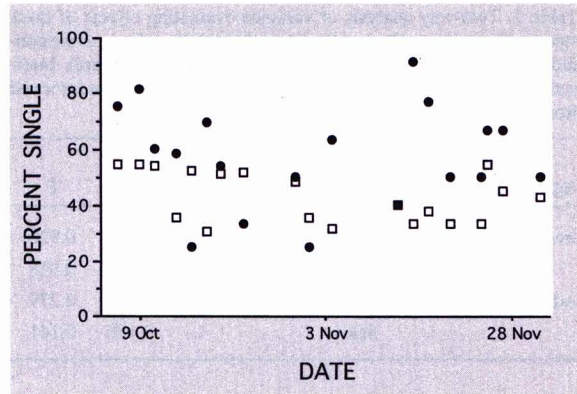


Figure 3. Percentage of single (i.e. lone) mallards comprising the hunting kill (solid circles) on 19 days during the 1989 hunting season and corresponding expected values (open squares) based on observation of the population at large.

the day. In addition, it is important to recognise that a given hunter might shoot more than one individual from the same flock. Thus, we presumably underestimated the proportion of singles comprising the hunting kill. Nevertheless, because we predicted *a priori* that hunters would take a disproportionately high number of singles, these considerations suggest that our test was conservative.

Despite the conservative nature of our test, our data indicate that single mallards were indeed overrepresented in the kill. On 15 of 19 days for which both hunter-collected and observational data were available, hunters took a greater proportion of singles than expected (Fig. 3). Collectively, these differences were highly significant (one-tailed Wilcoxon signed-ranks test, $T_s = 31$, $P < 0.005$). Thus, our data support the premise that single mallards are disproportionately vulnerable to hunting. However, we found no evidence whatsoever of a relationship between individual condition and flock status at the time of harvest (Tables 4 and 5).

Table 4. Condition (see Table 2) of hunter-shot juvenile and adult mallards classified according to sex and whether they were shot as singles or from flocks.

Age	Sex	Status	n	Condition	
				\bar{x}	SD
Juv	M	Single	126	10.37	0.86
		Flock	94	10.42	0.74
	F	Single	113	10.42	0.82
		Flock	70	10.37	0.86
Ad	M	Single	110	12.30	0.73
		Flock	71	12.32	0.76
	F	Single	76	12.09	0.77
		Flock	33	12.33	0.73

Table 5. Two-way analysis of variance evaluating effects of flock status (alone vs. in a flock at the time of harvest) and sex on the condition (see Table 2) of hunter-shot juvenile and adult mallards. Interactions were not significant ($P > 0.05$) and were therefore removed from each model.

Age	Model		Source	df	F	P
	n	r ²				
Juv	403	0.00	Single vs. flock	1	0.008	0.928
			Sex	1	0.011	0.918
Ad	290	0.01	Single vs. flock	1	1.177	0.279
			Sex	1	2.176	0.141

Discussion

Time of day

Our results indicate a clear and consistent diurnal pattern of harvest among mallards killed by hunters at Long Point, with peak harvest occurring during the first third of the day and with relatively little hunting mortality occurring at mid-day. A likely explanation for this pattern is that mallards staging at Long Point exhibit diurnal patterns of activity (i.e. movement) and that, consequently, more ducks are shot at certain times of the day than at others. This interpretation is based on a number of considerations. First, hunters using the WMU are required to hunt from a limited number of permanent blinds or shooting points. Thus, at Long Point, hunters necessarily employ a "sit-and-wait" strategy, and consequently, ducks should only be vulnerable when they are in flight. Secondly, our observation that few mallards were shot at mid-day is consistent with the general observation that staging and wintering waterfowl are often largely inactive at that time (e.g. Thornburg 1973, Paulus 1984, Thompson et al. 1988, see Paulus 1988 for a review). Thus, we believe that the diurnal patterns of harvest that we observed reflect genuine diurnal patterns of activity among staging mallards.

A critical assumption of our study was that hunters accurately reported times at which individual ducks were shot. Although hunter surveys can yield inaccurate data (e.g. Mikula et al. 1972, Hopper et al. 1975), problems most often arise when questions relate, directly or indirectly, to compliance with hunting regulations (see Metz & Ankney 1991). In our study, inquiries were unrelated to regulations and consequently, hunters had no obvious incentive to provide false information. Any inaccuracy therefore would have contributed random "noise" variation to analyses, and yet we found significant and consistent differences in harvest relative to time of day. Thus, even if accuracy of the information provided by hunters was not absolute, it is unlikely that our general conclusions would have been affected.

Despite pronounced diurnal variation in size of the kill, we found no evidence to suggest that mallards shot during non-peak periods were in relatively poor condition. This is surprising given the importance of premigratory fattening to staging waterfowl. Lipid reserves provide the primary fuel for migration (Blem 1990), and several studies have shown that condition can be an important determinant of over-winter survival (Haramis et al. 1986, Conroy et al. 1989, Bergan & Smith 1993). These factors are presumably responsible (at least in part) for the dramatic increases in body weight and lipid reserves typically exhibited by waterfowl during autumn (e.g. Ankney 1982, Reinecke et al. 1982, Hanson et al. 1990). Thus, individuals with limited fat reserves at this time of year should seek to improve their condition and should modify their behaviour accordingly. Our failure to detect a relationship between condition and time of day among hunter-shot mallards suggests that if such behavioural modifications do occur, they apparently do not include gross changes in diurnal patterns of activity. It remains to be determined why some mallards expose themselves to the risk of hunting mortality at a time of day when most individuals in the population are inactive.

Flocking behaviour

Our results indicate that single mallards comprised a greater proportion of the hunting kill than expected based on their representation in the population at large. There are two potential explanations for this observation. First, hunters might simply be more successful, on average, when attempting to shoot a lone bird than when attempting to shoot a bird from a flock. Alternatively, hunters might actually encounter lone birds at a disproportionately high rate. Two lines of evidence suggest that the latter explanation is more likely. First, based on observations made from "spy-blinds", Hochbaum & Walters (1984) concluded that individual hunters were no more likely to be successful (i.e. shoot one bird) when firing at a small flock than when firing at a large flock. Their analysis of flock size included lone birds. Secondly, previous studies have established a relationship between flocking behaviour and hunting vulnerability without relying on hunter-shot samples. For instance, using simulated hunts, Olson (1964) demonstrated directly that canvasbacks occurring alone or in small flocks decoyed more readily and more often flew within shooting range than those occurring in large flocks. Similarly, using spy-blind data, Boyd (1971) calculated that nearly 80% of flocks flying within shooting range contained five birds or less. Almost half of these small "flocks" were in fact lone birds (see Boyd 1971: Table 7). Although Boyd's (1971) study lacked a control sample for comparison, his results nonetheless suggested that hunters were encountering a disproport-

tionately large number of small flocks. Thus, our finding that single mallards were overrepresented in the hunting kill probably reflects a tendency on the part of lone birds to decoy more readily.

Factors responsible for the increased vulnerability of lone mallards have not yet been determined. Our expectation was that the relationship might be mediated by condition differences among individuals, as it is now well established that ducks in poor condition are disproportionately vulnerable to hunting (Greenwood et al. 1986, Hepp et al. 1986, Reinecke & Shaiffer 1988, Conroy et al. 1989, Dufour et al. 1993a, Heitmeyer et al. 1993). However, we found no evidence to suggest that single mallards were in poor condition relative to those shot from flocks. In this regard our results differ from those of Bain (1980), who demonstrated that such a relationship exists among both canvasbacks and redheads staging at Long Point. Although we can only speculate as to why our results differ from those of Bain (1980), the discrepancy might be attributable to differences in feeding ecology among the species examined. Specifically, diving ducks (tribe *Aythiini*) such as canvasbacks and redheads are highly gregarious during the non-breeding season (Johnsgard 1975) and as such, individuals probably rely heavily on each other for food finding. This might accentuate condition differences between single and flocked birds. Regardless, our results on mallards (tribe *Anatini*) suggest that relationships between flocking behaviour and vulnerability to hunting are not necessarily restricted to divers. Our findings further suggest that increased vulnerability of lone ducks can occur in absence of any relationship between flocking behaviour and condition. The specific mechanism(s) responsible for the high relative vulnerability of lone mallards remains a subject for future study.

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