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Research Article

Harvest Dynamics and Annual Survival of Mallards and Grey Ducks

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ABSTRACT We examined how hunter behavior, environmental covariates, and mallard (*Anas platyrhynchos*) and grey duck (*A. superciliosa*) population indices affected per capita harvest, hunter effort (i.e., hours hunted), and hunter participation (i.e., license sales) between 1997 and 2012 in the Eastern Fish and Game Region of New Zealand. Additionally, we examined how total annual hunter effort and harvest affected annual survival and harvest rates (i.e., the proportion of the population that is harvested). Per capita harvest increased with hunter effort and bag limits; hunter effort decreased over time, but effort and participation increased with mallard population size. Juvenile harvest rates were greater than for adults and negatively associated with population size. The relationship between harvest regulations and harvest rates was inconsistent. The 44-day seasons had greater juvenile harvest rates than the 57- and 72-day seasons. Similarly, years with a 7-bag limit had higher juvenile harvest rates than years with a 10-bag limit. Hunter effort affected annual survival rates, especially for females. Alternatively or concordantly, hunter effort may be a surrogate for population size and thus, survival rate may have been density dependent. The relationship between harvest and density-dependent mortality may in part be augmented by hunter behavior; fewer hunters hunted for fewer hours in years with relatively few birds. Our results suggest bag limits are more effective than season length at managing harvest; reducing bag limits to <2 birds/day from ≥ 7 could decrease harvest by as much as 50%. Furthermore, regulation consistency, better education, and enforcement of season regulations may improve harvest management; 58% of active hunters reported they shot mallards or grey ducks after the close of the 31-day season, which accounted for 13% of total harvest. © 2017 The Authors. *Journal of Wildlife Management* Published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

KEY WORDS *Anas platyrhynchos*, *Anas superciliosa*, grey duck, harvest regulations, hunter behavior, mallard, New Zealand, survival.

Hunters introduced mallards (*Anas platyrhynchos*) as a game bird to New Zealand (NZ) in the 1860s (McDowall 1994) to augment harvest of the native grey duck (*A. superciliosa*). Following a slow establishment phase (Williams 1981), legal mallard harvest began in 1931 and it is now the principal game bird in NZ (Caithness 1982, Williams 1999) attracting approximately 40,000 hunters annually. Mallards and grey ducks are combined during harvest data collection and for management purposes because it is difficult for hunters to distinguish between female mallards and grey ducks, and there is a large amount of introgression between the species (Rhymer et al. 1994, Rhymer and Simberloff 1996); thus, we pool data from both species in this paper. Although no comprehensive nationwide population estimates exist for mallards or grey ducks, there is a perceived population decline particularly in some North Island Fish and Game regions (P. Teal, New Zealand Fish and Game, Wellington Region, unpublished report). Since 1992, per capita mallard and grey duck harvest has declined across all Fish and Game regions, possibly because of declining duck populations or a decline in average annual hours hunted over the same time period (M. Rodway, New Zealand Fish and Game Southland Region, unpublished data). Consequently, the size of mallard and grey duck populations may affect hunter participation, effort, and retention with implications for license sales that support waterfowl population management. In turn, land-use change, climate change, and overharvest have the potential to affect mallard populations in NZ, but to date mechanisms behind observed trends remain unclear. Thus, managers are increasingly interested in better understanding the relationship between harvest, hunter behavior, and mallard and grey duck populations across NZ.

Unlike North America, NZ currently does not employ an adaptive harvest management (AHM) approach to waterfowl harvest, which is a transparent decision-making process that can incorporate multiple hypotheses regarding relationships between harvest and population dynamics (Johnson et al. 2015). Rather, 12 regional Fish and Game Councils are charged with managing game bird harvest, which includes mallards and grey ducks, in their region. This includes setting

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annual harvest regulations to maintain and improve the game bird resource. Population dynamics of NZ mallards and grey ducks are poorly understood and thus, harvest regulations are currently set with little information regarding their impact to populations (McDougall 2012). Council recommendations occur largely independently among regions and harvest regimes have not been evaluated for effectiveness in NZ. Regions regulate harvest in 3 ways: 1) constant regulations from year to year; 2) varied periodically based on perceived status of the population, and or, derived from what Councils believe hunters want; and 3) via regulation packages that are coupled to the regional combined mallard and grey duck population size or population trends.

Two of the most widely used methods of controlling harvest are hunting season length and bag limits (i.e., max. allowable daily harvest). Managers assume bag limits regulate daily take and season length controls the number of days hunters can hunt, effectively limiting total effort. Hunter effort (i.e., per capita hours hunted/season) and harvest rates (i.e., the proportion of the population that is shot and recovered; an index of kill rate) can be influenced by substantial changes in season length and bag limits (Nichols and Johnson 1996), but the link is imperfect (Johnson and Case 2000).

In North America, consequences of harvest rates on annual survival rates have led to debate (Anderson and Burnham 1976, Nichols and Hines 1983, Burnham and Anderson 1984, Sedinger and Rexstad 1994, Smith and Reynolds 1994) and show mixed results (Nichols and Johnson 1996). A recent review suggests harvest can substantially affect waterfowl population dynamics, but effects are complex and vary by species and through time and space (Cooch et al. 2014). In NZ, Barker et al. (1991) examined the consequence of hunting mortality on natural mortality of grey ducks. They rejected the hypothesis that hunting mortality was completely compensated by natural mortality and determined hunting mortality was at least partially additive, concluding that restrictive regulations may positively affect annual survival.

New Zealand provides a unique opportunity to investigate some of the more perplexing issues surrounding waterfowl harvest management. Mallards in NZ are relatively sedentary and do not migrate (Balham and Miers 1959); this population homogeneity makes it easier to establish the effects of externalities such as harvest regulations on population dynamics (Martin and Carney 1977). Second, harvest recoveries are confined to a single country and normally within a limited geographic range; 86% of band recoveries in the Eastern Region are within 50 km of the band site (McDougall 2012). Thus, the impact of harvest regulations is generally consistent within mallard subpopulations. Lastly, habitat conditions appear relatively stable among years (although the quality of the habitat may vary). Therefore, annual recruitment in NZ may not be subject to seasonal habitat availability unlike some parts of the United States and Canada such as the Prairie Pothole Region, where production appears to be a function of the number of breeding mallards and inundated wetland areas (Crissey 1969, Dzubin 1969, Anderson 1975, Howerter et al. 2014).

We used 16 years (1997–2012) of hunter survey and band recovery data in the NZ Eastern Fish and Game Region to evaluate how different levels of combined mallard and grey duck harvest regulation (season length and bag limits) affected hunter effort, annual survival, and annual harvest rates. Preliminary analyses in the same area suggested little association between regulations and harvest rates (McDougall 2012). Therefore, we suspected season length and bag limits used in the Eastern Fish and Game Region may also poorly govern total harvest, hunter effort, and hunter participation.

STUDY AREA

The Eastern Fish and Game Region encompasses approximately 31,000 km^2 of the North Island of New Zealand (38°28′ 39″S 177°05′ 30″E; Fig. 1). The majority of the region is upland and described as central hill country and volcanic plateau, with a coastal lowland on the northern and eastern margins (Leathwick et al. 2003). Several volcanic-derived, moderate size (>1.4 km^2) oligotrophic–eutrophic lakes dominate the central upland and support low to moderate densities of mallards and grey ducks. Low densities of waterfowl predominate the eastern zone of the region in numerous small (<1.5 ha) livestock ponds and lowland rivers (M. B. McDougall, NZ Eastern Fish and Game, unpublished report). Intensive agriculture (dairy) and horticulture (kiwifruit) dominate the historically wetland-rich northern lowlands (<100 m ASL; Irving and Beadel 1992). Drainage ditches in these lowlands are important brood-rearing areas and the few remnant wetlands are valued for game bird hunting. Mallards are the predominant game bird. Vegetation composition of the study area reflects the predominant

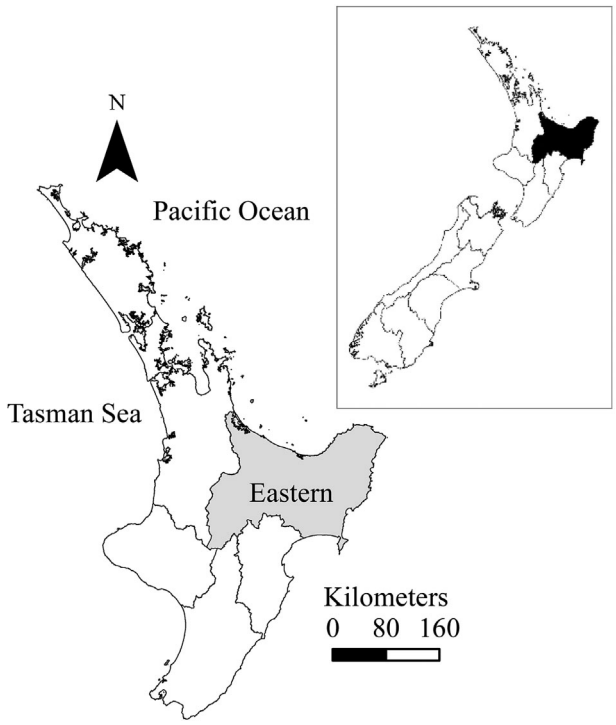

Figure 1. New Zealand's North Island Fish and Game regional boundaries.

land use, topography, and climate (Leathwick et al. 2003). The hill country is pastoral interspersed with production forestry (radiata pine [*Pinus radiata*]) and stands of remnant native forest. Lowland is a combination of more intensive agriculture (pastoral) and horticulture. The volcanic plateau is dominated by alpine vegetation, pastoral, and production forestry. New Zealand seasons are summer (Dec–Feb), autumn (Mar–May), winter (Jun–Aug), and spring (Sept–Nov). The start date of the hunting season is the first weekend in May and the end date typically occurs shortly before or after the onset of nesting in August (Marchant and Higgins 1991).

The procedure for setting season regulations in the Eastern Region varied over the study (1997–2012). For the first 2 years (1997–1998), regulations were derived from the perceptions governors had of the mallard and grey duck population size and reports from hunting clubs. In 1999, season regulations were essentially the same as the 2 prior years. In subsequent years, regulations were set as a function of population size (Lincoln estimate; Alisauskas et al. 2013) in year t-1, survival from year t-1 to year t, and productivity estimates in year t. In these years, regulations (i.e., season length and daily bag limit) were based on 3 restraint levels: restrictive (when the population was assessed at <400,000 birds), intermediate (≥400,000 and <550,000 birds), and liberal (≥550,000 birds). However, the regulation set that applied to each degree of restraint varied over the study period resulting in very little association between levels of restraint and regulations (Table 1).

METHODS

Harvest Survey

New Zealand game bird hunters are required to record contact details when they purchase a license to hunt game birds. This provides a representative sample of all hunters from which to derive harvest and effort data. New Zealand Fish and Game has conducted a national hunter survey annually since 1992 (Barker 1991, Barker and MacKenzie 1999). The game bird season is divided into 7 survey periods: opening of the game bird season (the first weekend = period 1) and fortnightly for periods 2–5 (dabbling duck season), and monthly at close of the dabbling duck season (periods 6 and 7, which cover other game birds such as ring-necked pheasant [*Phasianus colchicus*]). We randomly sampled Eastern Region licensed hunters ($n = 120$) for each of the 7 periods during the game bird season and interviewed hunters by phone (1997–2013) (i.e., 840 interviews for each region per year). We asked hunters 1) on which dates they hunted during the period; 2) how many hours they hunted waterfowl and upland game (e.g., pheasant, California quail [*Callipepla californica*], and brown quail [*Synoicus ypsilophorus*]); 3) the number of each species shot; 4) how many shot birds were not recovered; and 5) the area in which they hunted (including which Fish and Game Region). We also recorded licensed hunters that did not hunt during the period. Eastern Region survey data showed that some hunters continued to report shooting mallards and grey ducks after the dabbling duck season had finished so we separated analyses into hours spent hunting waterfowl during the dabbling duck season and the combined mallard and grey duck harvest 1) during this interval; and 2) during this interval and after the season only for the days in which hunters reported shooting mallards or grey ducks.

We estimated mean ($\bar{y}$) per capita harvest, hours hunted, and days hunted for all licensed game bird hunters in the Eastern Region for each survey period i ($i = 1, \ldots, 7$) and year j ($j = 1997, \ldots, 2012$) and estimated standard error from sample variance (σ^2) and sample size (n) where $\mathrm{SE}(\bar{y}_{ij}) = \sqrt{\sigma^2_{ij}/n_{ij}}$. We estimated population sizes by multiplying sample means (and SE) by the number of licensed hunters.

Table 1. License sales (an index of hunter participation), season regulations (season length, daily bag limit), and harvest regime based on the Eastern Region mallard population size (fixed, restricted if $\hat{N}$ <400,000, intermediate if $\hat{N}$ ≥400,000 and <550,000, and liberal if $\hat{N}$ ≥ 550,000) from 1997–2012 in the Eastern Fish and Game Region, New Zealand. From 2001–2006 season length was fixed to 58 days and bag limit was used to regulate harvest.

Yr	License sales	Season length (days)	Daily bag limit	Harvest regime
1997	3,641	72	15	Fixed
1998	3,641	72	15	Fixed
1999	3,729	72	15	Fixed
2000	3,765	44	10	Restricted
2001	3,550	58	7	Restricted
2002	3,613	58	7	Restricted
2003	3,938	58	7	Restricted
2004	3,956	58	10	Intermediate
2005	3,793	58	10	Intermediate
2006	3,489	58	10	Intermediate
2007	3,992	72	10	Intermediate
2008	3,958	58	7	Restricted
2009	3,835	31	10	Intermediate
2010	3,821	58	10	Intermediate
2011	3,956	58	10	Intermediate
2012	3,683	44	10	Restricted

Hunter Effort and Harvest

We defined hunter participation as the number of annual licenses sold in the Eastern Region each year. We derived total harvest and hunter effort from harvest surveys and used hours hunted per year to measure hunter effort rather than days hunted because a large proportion of the harvest occurs during the first 2 days in the season.

We defined annual harvest rates (h) as the proportion of the population that were shot and recovered each year. If a portion of the population is marked, harvest rates may be estimated from the proportion of the marked animals that are killed provided the marked animals are representative of the population of interest (Anderson 1975). To estimate harvest rate from banded waterfowl, the shot bird has to be recovered and reported. The reporting rate can vary annually and geographically (Reinecke et al. 1992, Pollock et al. 1994, Nichols et al. 1995) and therefore needs to be established.

We trapped mallards and grey ducks (Jan–Mar) with walk-in funnel traps (McDougall 2012), aged birds (juvenile = hatch

year, adult = after hatch year) from cloacal examination (Taber 1971), and marked them with individually numbered stainless steel leg bands at 14 discrete sites in the Eastern Region, 1997–2013. We trapped and handled birds in accordance with the Bird Bander's Manual (Melville 2011), which meets legal obligations of the Animal Ethics Committee Department of Conservation and, New Zealand legislation (Animal Welfare Act 1999, Wildlife Act 1953, and Wildlife Regulations 1955). Certification of the lead author to supervise and band game birds was provided by the Department of Conservation Banding Scheme (certificate no. 2013/096). Previous studies reported higher recovery rates (the bird is shot, recovered, and reported) for juvenile than adult mallards and grey ducks in NZ (Nichols et al. 1990, Caithness et al. 1991); therefore, we calculated age-specific harvest rates (h_{ij}; $i \in$ {adults, juveniles}) from the direct recovery of banded birds (recovered in the year they were banded; $n = 1{,}709$) and adjusted for annual reporting rate. In the last survey period of each year, we asked hunters if they had shot a banded bird in year j, $j-1$, and $j-2$, and if they reported it in year j, $j-1$, or $j-2$. We were mindful of recall bias (Barker 1991) but considered shooting a banded bird would be an extraordinary event. We estimated reporting rate as

$$\lambda_j = \frac{R_j}{(R_j + NR_j)} \quad (1)$$

where R and NR represent the number of bands reported or not reported, respectively, in year j ($j = 1997,...2013$). We randomly selected 129 surveys during 5 years of our study (i.e., 1997, 2004–2005, 2011–2012) and cross checked survey records against the band reporting database for survey participants and members of their household that also held game bird licenses to verify reporting rates.

Next, we estimated harvest rate as

$$h_{ij} = \frac{m_{ij}}{R_{ij}} \frac{1}{\lambda_j} \Psi \quad (2)$$

where h_{ij} is the harvest rate (probability that a bird is shot and recovered) in year j for age class i representing adults (after hatch year) or juveniles (hatch year), R_{ij} is the number of adults or juveniles banded in the Eastern Region in year j, m_{ij} is the number of direct recoveries (adults or juveniles banded and shot in year j and reported to NZ Fish and Game), and λ_j is the reporting rate in year j. The probability that banded birds remained in the harvest region (ψ) was high based on recorded harvest locations ($\hat{\psi} = 0.983 \pm 0.003$ [SD]); therefore, we set ψ to 1.0.

Covariates.—We evaluated several factors potentially affecting variation in hunter participation (license sales), hunter effort (hours hunted), total harvest, and harvest rates including year, season length, bag limit, and either population size estimated for the Eastern Region ($\hat{N}$) or an index of population size (T; Table S1). For hunter effort, we calculated $\hat{N}$ using a Lincoln estimator per Alisauskas et al. (2013) except within a Bayesian framework (M. B. McDougall, unpublished report). The Wellington population index (T) represented the average total count from aerial transect surveys obtained from the closest NZ Fish and Game region that had an index of annual population size for the entire study period (P. Teal, New Zealand Fish and Game Wellington Region, unpublished data; Fig. 2). We included T as a covariate in participation, harvest, and harvest rate models because harvest and license sales are used to estimate $\hat{N}$ and thus, would be using the data twice (Alisauskas et al. 2013).

We evaluated the potential influence of 2 additional covariates on hunter effort including opening weekend success, defined as the number of mallards and grey ducks harvested per hour per hunter over those 2 days, and relative climate as an interaction between mean winter (i.e., hunting season) precipitation and mean winter temperature (Whakatane Aero Weather Station; National Institute of Water and Atmospheric Research 2013). We evaluated 3 additional covariates on harvest: mean per capita hours hunted (hours hunted), mean per capita days hunted (days hunted), and sinusoidal trend through time. We considered that harvest and harvest rates may be cyclical and therefore included the sinusoidal trend covariate given that population size estimates and Wellington Region aerial counts appeared to oscillate over the study period (Fig. 2). Harvest rates may oscillate if harvest is relatively constant among years (hunters may strive to harvest a similar number of birds each year), but the population fluctuates over time causing harvest rate to also fluctuate. We postulated that harvest rates could also be influenced by the number of hunters (estimated from license sales), annual harvest, hours hunted, days hunted, and precipitation prior to the opening of the hunting season (Apr rain in mm); heavy precipitation prior to the beginning of the game bird season can create ephemeral wetlands away from traditional mallard hunting sites making birds less available for harvest.

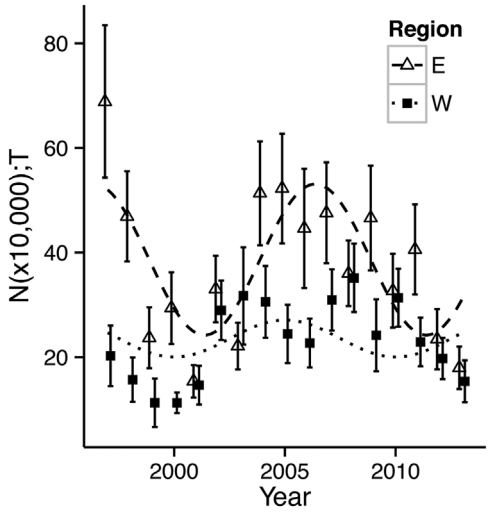

Figure 2. An index of mallard and grey duck population size in the Wellington Fish and Game Region (W) from aerial transect counts (T; $\bar{x} \pm 85\%$ CI; dotted line = 17-yr cyclic trend) and Eastern Fish and Game Region, New Zealand (E; $\hat{N}$/10,000; $\bar{x} \pm 85\%$ Bayesian CI; dashed line = 10-yr cyclic trend).

Statistical analysis.—We built general linear models for hunter participation, hunter effort, and total harvest in package Stats in Program R, version 2.15.2 (R Development Core Team 2015). We estimated harvest rate and reporting rate in a Bayesian framework using WinBUGS software (Lunn et al. 2000). Bayesian analysis allowed us to model reporting rate as a binomial distribution using an informative beta-distributed prior on λ where the shape parameters were a function of the average verified reporting rate ($\bar{x} = 0.62 \pm 0.094$) from 24 surveys conducted outside of the study period (2013–2015; prior distribution for $\lambda \sim$ Beta [15.96, 9.96]; Fig. S1). We used a uniform prior for harvest rate and constrained it to $0.04 > h < 0.5$ because previous analysis (McDougall 2012) reported harvest rates in the Eastern Region ranged from 0.07 to 0.21. We ran 1 million iterations, 3 chains, and discarded the first 1,000 as burn-in (Gelman and Rubin 1992). We checked trace plots for convergence. We checked the accuracy of the posterior estimates such that the Monte Carlo error/sample standard deviation <0.05. To estimate the 85% Bayesian credible intervals (BCI), we conducted bootstrap simulations that consisted of 100,000 random draws from a beta distribution with mean harvest rate and standard deviation in Program R (R Development Core Team 2015). We used 85% confidence limits and BCIs to maintain consistency with Akaike's Information Criterion (AIC) model selection (Arnold 2010).

Survival Analysis

We estimated annual survival from banding data in Program MARK (White and Burnham 1999) using the Burnham live recapture–dead recovery module (Burnham 1993). This module allows the encounter probabilities to be modeled as a function of the joint probabilities that a bird survived from time t to $t+1$, a bird was recaptured (p_t), if a bird was killed that the band was found and reported (the conditional reporting rate, r_t), and a bird showed fidelity (F_t) to the study area (i.e., it was available for recapture; Cooch and White 2006). We derived summary encounter histories for each cohort based on release year, age, and sex.

We denoted climate covariates as the average rainfall and temperature for the 3 months prior to year j (Oct, Nov, and Dec); mean spring rainfall and temperature in year j (current yr); the average rainfall and temperature for June, July, and August (i.e., winter rain or temp); and the average rainfall and temperature for December in year $j-1$, and January and February in year j (i.e., summer rain or temperature, respectively). Climate covariates were aligned with probable stress events in the annual cycle such as molt and breeding (McDougall 2012). Harvest covariates included days hunted, hours hunted, and harvest reported from the game hunter survey.

We constrained survival to a linear function of covariates for climate, harvest, an index of population size (T), time, age, and sex. For all models, we constrained conditional reporting rate to age and time effects given that juveniles are more likely to be shot and reported than adults (Nichols et al. 1990, Caithness et al. 1991). We set recapture and fidelity parameters to vary by sex, age, and time period (e.g., group × t) to limit the number of models considered (Anderson et al. 2001).

Harvest rates are indexed to recovery rates (Francis et al. 1998) where recovery rate is defined as the probability that the bird is killed by a hunter, retrieved, and reported (Brownie et al. 1985). Under the Burnham live-dead parameterization (Burnham 1993), when the majority of mortality is associated with harvested birds we assume the conditional reporting rate (the marked animal is recovered and reported; Seber 1970) also indexes harvest rate and therefore may be influenced by season regulations and harvest. We therefore ran a second set of analyses where the conditional reporting rate of the most supported model was constrained to a function of bag limit, season length, and harvest.

Model Selection

We created *a priori* sets of general linear models to evaluate possible covariate effects on unique response variables. We selected biologically plausible linear combinations and interactions of the covariates described above in addition to intercept-only models (Tables S1 and S2). We evaluated 9 hunter participation, 21 hunter effort, 22 harvest, 33 harvest rate, and 51 survival models based on preliminary analysis (McDougall 2012).

We ranked models using Akaike's Information Criterion adjusted for small sample size (AIC_c) and reported results relative to the most supported model (ΔAIC_c). We evaluated informative parameters (i.e., the addition of the parameter to a model did not increase AIC_c by more than 2 units; Arnold 2010) from models with some empirical support ($\Delta AIC_c < 10$; Burnham and Anderson 2002) and report means with 85% credible or confidence limits (Arnold 2010). The use of information-theoretic approaches for Bayesian model selection are often problematic for hierarchical mixed models (Laud 2013). However, we chose AIC model selection for our Bayesian analysis of harvest rates to be consistent with analyses of other response variables and because for our relatively simple model structure, AIC provides good predictive power and produces results very similar to other typically Bayesian information criteria (Hooten and Hobbs 2015).

For survival models, we determined data fit on the most parameterized model (full model) with 100 bootstrap simulations (White et al. 2001). Further, we suspected some over-inflation of the variance due to birds staying together following banding thus violating the assumption that encountering a banded bird is an independent event (Brownie et al. 1985, Nichols 2005). Therefore, we accounted for overdispersion in the data using a variance inflation factor ($\hat{c}$) using the median $\hat{c}$ test in Program MARK (Stafford and Aaron 2007). We then ranked survival models only by AIC_c adjusted for overdispersion (i.e., $QAIC_c$; White et al. 2001, Burnham and Anderson 2002).

RESULTS

The estimated mallard-grey duck population ranged from 746,000 in 1997 to 172,000 in 2013 (M. B. McDougall,

unpublished report; Fig. 2). During that period bag limits were 7, 10, or 15 birds/day, and season length ranged from 31 to 72 days (Table 1).

Participation

On average, 3,773 ± 160 (SE) people purchased licenses annually and license sales were positively associated with the Wellington Region mallard and grey duck population index (Akaike weight [w_i] = 0.55; β = 12.17, 85% CI = 5.56–18.79; Table S3). On average, 73% (range = 63–81%) of license holders hunted waterfowl over the opening weekend; the remainder hunted upland game (pheasant or quail) or did not hunt. Active waterfowl hunters dropped to 48% (range = 37–61%) in the next 2 weeks and curtailed to 4% (range = 0–10%) by the last survey period (Fig. S2).

Hunter Effort

Mean annual per capita hours hunted was 20.37 and ranged from 14.26 to 27.86 hours (Table S4). A large portion of hours hunted ($\bar{x}$ = 42%; range = 38–49%) occurred over opening weekend, which also accounted for an average of 44% (range = 38–55%) of mallard and grey duck harvest. This large concentration of effort at the beginning of the season was followed by a sharp drop off in hunter effort, which was a function of a decrease in active hunters (Fig. S2), a decrease in average daily hours hunted (Fig. S3), and a decrease in average number of days hunted (Fig. S4). The most supported model (N + yr; w_i = 0.59; Table S5) suggested average annual hours hunted increased as a function of population size (β = 8.74e-06; 85% CI = 4.73e-06–1.27e-05) and decreased with year (β = −0.497; 85% CI = −0.63 to −0.363). On average, a decrease in the mallard-grey duck population of 75,000 birds over 1 year would reduce hunter effort by approximately 5%. This model fit the data reasonably well with only 2 years where predicted hunter effort was not within the 85% confidence interval of observed effort (Fig. 3). Changes in average hours hunted were not well explained by season length or bag limit; including the season length or bag limit covariate with the most supported model reduced fit ($\Delta AIC_c > 2$; Table S5).

Annual Harvest

Annual mallard and grey duck harvest averaged 41,500 birds (range = 24,600–61,200). During the first 2 years of the study, hunters shot considerably more birds than subsequent years (Fig. 3), but there was no model support for changes in per capita harvest (including harvest reported after the close of the season) by year (ΔAIC_c = 79; Table S6). Harvest was best explained (w_i = 0.51) by a combination of hunter effort (β = 0.52, 85% CI = 0.31–0.72) and bag limits (β = 0.39, 85% CI = 0.130–0.647). Interpolation of this model suggests a 10% change in the average annual hours hunted for the study period would result in a change of 1 mallard harvested per hunter seasonally, whereas an increase in bag limit from 7 birds to 10 and 15 birds would result in 1.2, and 3.1 more mallards harvested per hunter per season, respectively. All but one of the models that included hours hunted received some support ($\Delta AIC_c < 5$). Furthermore, the bag limit-×hours hunted model received some support (ΔAIC_c = 3.04, w_i = 0.11), but the effect of hours hunted on per capita harvest did not vary substantially by bag limit (β = −0.039, 85% CI = −0.121 to 0.044).

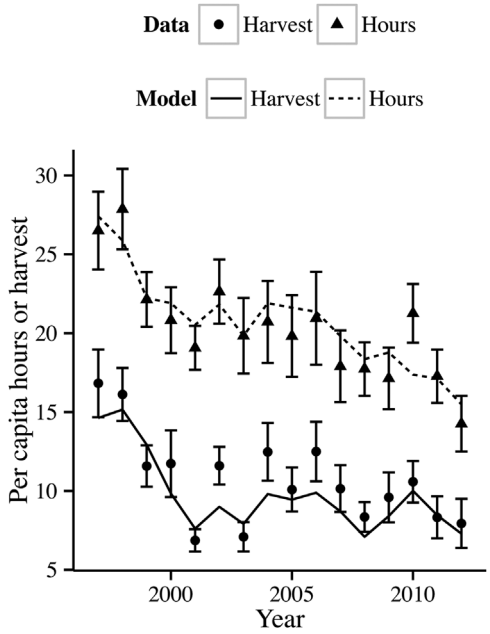

Figure 3. Per capita hours hunted and harvest ($\bar{x}$ ± 85% CI) of mallards and grey ducks in the Eastern Fish and Game Region, New Zealand, 1997–2012. Predictions were fit with the most supported models (dashed line, hr = mallard and grey duck population size + yr; solid line, harvest = hr hunted + bag limit).

For the majority of days hunted during 1997–2012 (68%; n = 10,279), hunters shot ≤2 mallards and grey ducks/day and on 92% of the days <7 were shot when the minimum bag limit during the study was ≥7. However, the other 8% of days when ≥7 mallards and grey ducks were reported shot accounted for 35% of the cumulative harvest (Fig. 4); the majority of this harvest (59%) occurred over opening weekend. Hunters reported shooting their limit on 5% of occasions when the bag limit was 7, 3% when the bag limit was 10, and <1% when the bag limit was 15. The percentage of hunters that reported shooting more than the daily bag limit was small (2%, 1%, and <1% for bag limits of 7, 10, and 15, respectively), but this accounted for a relatively high percentage of the total reported harvest (10%, 7%, and <2% for bag limits of 7, 10, and 15, respectively). During the 31-day season 58% of active hunters reported shooting mallards or grey ducks after the end of the dabbling duck season, which accounted for 13% of the total harvest. Reported illegal harvest ranged between 0–5.6% of the total harvest when season length was >31 days.

Reporting and Harvest Rates

Banding data during 1997–2013 comprised 336 and 1,214 direct (i.e., within year) recoveries obtained from 6,350 banded adults and 13,733 banded juveniles, respectively. We were able to verify reporting status for 69% of a sample of hunter surveys during our study years (n = 89 of 129) and for 62% of 39 surveys after our study period. Verified reporting rate during our study period was consistent with the overall reporting rate estimate ($\bar{x}$ = 0.60 ± 0.046 [SE] and $\bar{x}$ = 0.63

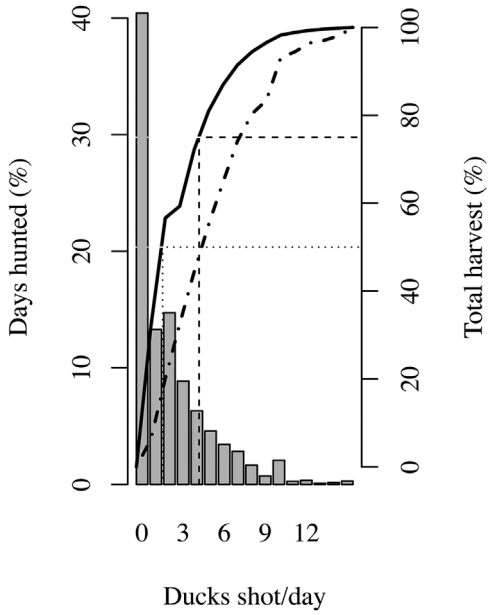

Figure 4. Percentage of days hunted in the Eastern Region, New Zealand from 1997–2012 ($n = 10{,}279$) where 0, 1, 2, ... 15 mallards or grey ducks/day were shot. For example on 40% of days hunted, hunters shot 0 ducks and on 13% of days hunters shot 1 mallard or grey duck. The right *y*-axis shows the cumulative harvest (%, dot-dash line). For example hunters that bagged ≤7 ducks/day accounted for 75% of the total harvest. The black solid line represents the estimated harvest under bag limits of 0, 1, 2, ... 15. For example bag limits of <2 and <5 represents 50% (dotted line) and 75% (dashed line), respectively, of the total harvest.

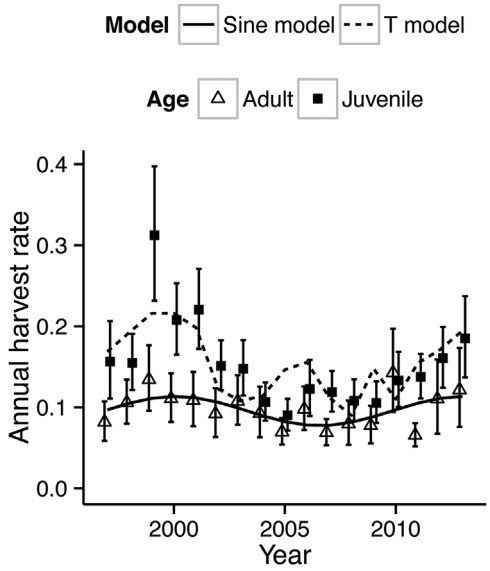

Figure 5. Harvest rates of adult (A), and juvenile (J) mallards and grey ducks ($\bar{x} \pm 85\%$ Bayesian CI), in the Eastern Fish and Game Region, New Zealand, 1997–2013. The solid line represents a 13-year sine cyclic trend for adults and the dashed line represents the relationship between juvenile harvest rates in the Eastern Region and Wellington Fish and Game Region aerial transect counts of mallards (T).

± 0.016, respectively). Juvenile harvest rates corresponded negatively ($\beta_{JUV} = -0.005$, 85% CI = −0.007 to −0.003) to the Wellington Region population index ($w_i = 0.35$; Fig. 5 and Table S7). If Wellington counts can be used as a proxy for Eastern mallard population size (Fig. 2), then this suggests juvenile harvest rates increase as the population decreases. For adults, the best-supported model was the sine model ($w_i = 0.16$; Table S8); however, this support was only marginally better than the license sales model ($\Delta AIC_c = 0.63$, $w_i = 0.12$). The period (wave length) was 12.98 years (85% CI = 12.97–12.99), with a mean wave height (i.e., harvest rate) of 0.095 (85% CI = 0.088–0.103). Adult harvest rates decreased with increasing license sales ($\beta = -5.27e\text{-}05$, 85% CI = −9.7e-05 to −8.4e-06). A 10% increase in license sales (hunters) results in an approximate 2% decrease in harvest rates.

Estimated harvest rates did not increase linearly with relaxing season regulation constraint. For seasons when the bag limit was 10, juvenile harvest rate under the 44-day season length ($\bar{x} = 0.18$, 85% BCI = 0.149–0.211) was greater than the harvest rate under the 58-day season length ($\bar{x} = 0.11$, 85% BCI = 0.101–0.122) and the 72-day season length ($\bar{x} = 0.126$, 85% BCI = 0.104–0.148). Similarly, for adults the 44-day season length had greater harvest rates ($\bar{x} = 0.106$, 85% BCI = 0.082–0.132) than the 58-day season length ($\bar{x} = 0.071$, 85% BCI = 0.061–0.082) but were similar to the 31-day season length ($\bar{x} = 0.086$, 85% BCI = 0.063–0.109) and the 72-day season length ($\bar{x} = 0.069$, 85% BCI = 0.053–0.085). Likewise under different bag limits with a fixed season length of 58 days, the 7-bird bag limit season had greater juvenile harvest rates ($\bar{x} = 0.15$, 85% BCI = 0.131–0.167) than the 10-bird bag limit season ($\bar{x} = 0.11$, 85% BCI = 0.099–0.125). Adult harvest rates in 7-bird bag limit seasons ($\bar{x} = 0.090$, 85% BCI = 0.075–0.107) were greater than 10-bird bag limit season ($\bar{x} = 0.071$, 85% BCI 0.061–0.082). Conversely, for a season length of 72 days, juvenile and adult harvest rates during 15-bird bag limit seasons ($\bar{x}_{juv} = 0.21$, 85% BCI = 0.172–0.240; $\bar{x}_{adult} = 0.11$, 85% BCI = 0.087–0.127) were greater than the 10-bird bag limit seasons ($\bar{x}_{juv} = 0.119$, 85% BCI = 0.094–0.145; $\bar{x}_{adult} = 0.069$, 85% BCI = 0.053–0.086; Fig. 6).

In our mark-recapture analysis, we evaluated 3 models incorporating either season regulations (bag limit, season length) or harvest in addition to age and time effects under the premise that these variables may index harvest rates. The 2 models that incorporated season regulations received the same support ($\Delta AIC_c = 2.036$, $w_i = 0.21$; Table S9), but the parameters were uninformative (Arnold 2010). Further, the model containing total harvest received no support.

Annual Survival

We obtained 865 live recaptures (during subsequent trapping occasions) and 2,526 recoveries from 20,433 mallards and grey ducks banded during 1997–2012. The most supported model suggested survival was greater for males and adults than for females and juveniles, and decreased with increased hours hunted ($w_i = 0.54$; Table S9). Furthermore, hunter effort had a greater effect on female survival (Table S10). Adult female survival was 0.63 (85% CI = 0.59–0.68), adult male survival was 0.66 (85% CI = 0.64–0.68), juvenile female survival was 0.49 (85% CI = 0.45–0.54), and juvenile male survival was 0.50 (85% CI = 0.49–0.51; Table S4).

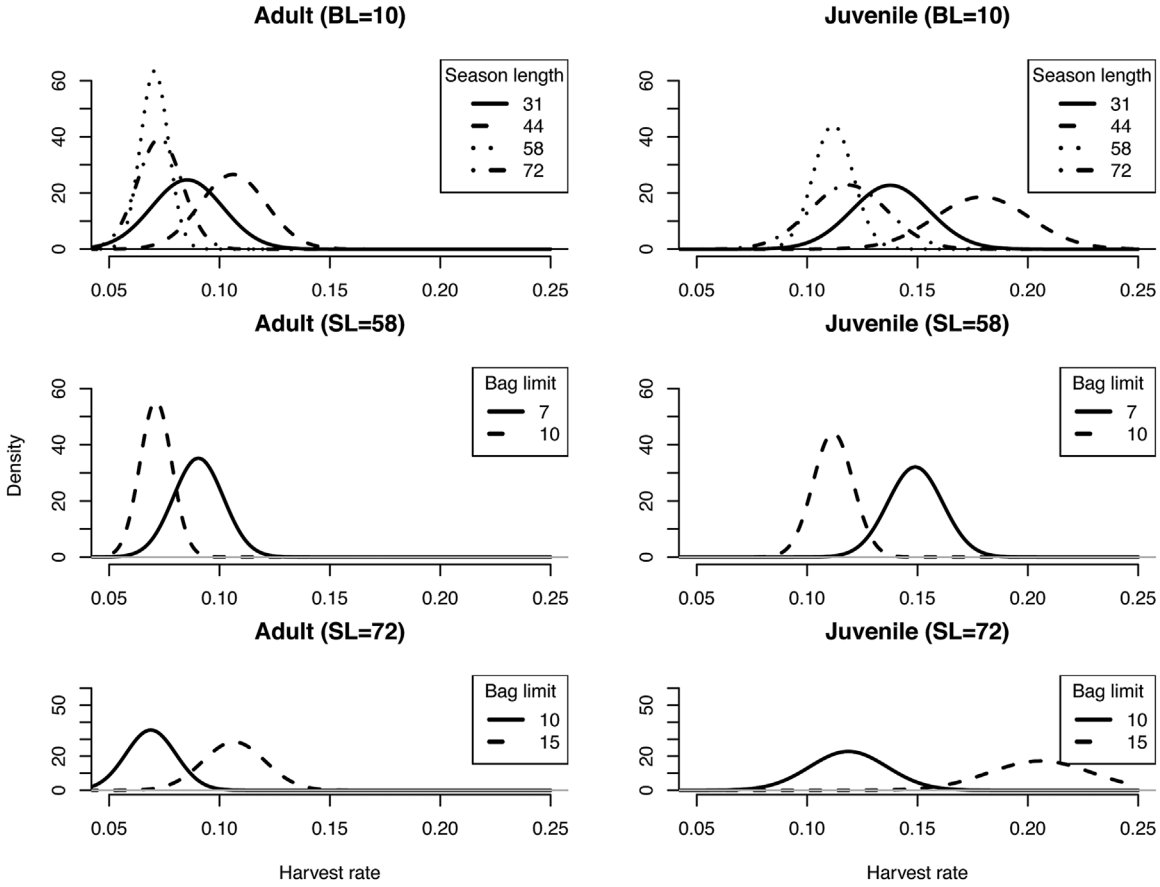

Figure 6. Juvenile and adult harvest rates (*h*; probability density functions) of mallards and grey ducks constrained to either bag limits (BL) of 10 birds or season lengths (SL) of 58 days and 72 days for adults and juveniles in the Eastern Fish and Game Region, New Zealand, 1997–2013.

Interpolation of the most supported model parameters indicated a 10% increase (~2 hr) in the average hunter effort for the period 1997–2012 reduced adult female survival by 0.08 (12%) and a 10% decrease in hunter effort increased survival by 0.07 (11%).

DISCUSSION

Our study provides valuable insight into the trends of hunter participation, hunter effort, and harvest rates in the face of variable waterfowl harvest regulations, with implications for waterfowl management across New Zealand. Our results support the notion that harvest and population size cannot be readily managed by regulating hunting through season length and bag limits (Johnson and Case 2000). The regulation set used in the NZ Eastern Region over the study period performed poorly at constraining annual per capita hours hunted. Furthermore, hunter effort reduced annual survival of mallards and grey ducks, which emphasizes the need for effective and adaptive harvest management to sustain waterfowl populations in the region.

Season limits had no effect on per capita harvest, partially because hunters continued to hunt after the close of the short seasons. Up to 10% of reported annual harvest was a result of hunters exceeding the daily bag limit during opening weekend and up to 13% of harvest occurred after the dabbling duck season ended. Similarly, Martin and Carney (1977) reported compliance in the United States was also poor when bag limits were relatively low (1–2 birds/day). Illegal harvest may be a product of insufficient enforcement; the Eastern Fish and Game Region employs approximately 10 full-time Fish and Game Officers to monitor roughly 3,500 active waterfowl hunters. However, because hunters routinely admitted to harvesting greater than daily bag limits or hunting outside the season dates during hunter surveys, confusion regarding annual regulations may have led to the illegal harvest observed in our study. Harvest regulations vary from region to region and hunters may hunt waterfowl across multiple regions, increasing confusion regarding season dates and limits. Furthermore, season regulations changed on average every 1.8 years during our study. Schroeder et al. (2014) reported that hunters can adapt to changes in season regulations, but it took approximately 4 years for waterfowl hunters in Minnesota, USA, to adapt to increased restrictions in season length and bag limits. Thus, consistency in regulations through time and space may improve compliance and the ability for regulations to control total harvest.

We found no evidence that hunter participation was associated with season regulations. Despite relatively stable participation, we found the hours spent hunting decreased through time, consistent with national trends and that reported by Otis (2004) for Canadian hunters. The decrease in hunter effort over the study may also explain the decrease

in harvest rather than a decrease in the mallard-grey duck population.

Decreasing hunter effort could be a result of other activities (e.g., hobbies) vying for hunters' time and warrants further examination (Brocklesby et al. 1995, Palmer and Whitfield 2009). Miller and Vaske (2003) reported that personal reasons like finances, free time, and hunter perceptions regarding the availability of game and severity of regulations predicted decreased hunter effort over time. Furthermore, Stafford et al. (2010) reported that waterfowl hunter success was influenced by local and breeding population size, which may in turn influence hunter effort. This may be explained by the law of diminishing returns whereby hunters hunt less when they are less successful and vice versa (Strickland et al. 1996). Our data did not support effects of opening weekend hunter success on hunter effort, but were consistent with Strickland et al. (1996) supporting the law of diminishing returns when observed against population size.

The mechanics influencing harvest rates are unclear. Similar to population size, harvest rates appear to oscillate over time and were negatively associated with the Wellington Region population index for juveniles. Juvenile harvest rates were greater and oscillated over a larger range than the adults, but we were unable to attribute changes in harvest rates to any season regulations, harvest, or hunter effort. Anecdotal evidence suggests hunters may spend more time hunting during short seasons, thus harvesting a greater proportion of the population (M. B. McDougall, unpublished data). This supposition is consistent with the high harvest rates in the 44-day seasons. The ratio of annual hours hunted to the estimated mallard population size in the 44-day seasons (0.25) was greater than any of the other season lengths (0.15, 0.20, 0.17 for season lengths of 31, 58, 72, respectively). The 31-day season had the lowest number of hours hunted as a proportion of $\hat{N}$ possibly indicating that this season length is starting to restrict hours hunted.

Care must be taken in interpreting the harvest rate results because harvest rate is confounded with reporting rate. We were unable to substantiate 31% ($n = 129$) of interviews where hunters claimed to have reported a band, but the report was missing in the banding database. An Auckland-Waikato Region study (Auckland-Waikato Fish and Game, unpublished data) reported bands missing from the database were some combination of non-reporting and reporting done by someone other than the license holder (e.g., hunting partner, family member, cohabitant). However, that study reported false reporting rates (determined from follow up surveys of participants with missing band reports) were similar to our estimates in some years. Misreported bands can bias recovery rates, and subsequently harvest rates and population estimates using band recoveries (Wright 1978, Alisauskas et al. 2013). However, verified band reports in and out of our study period were similar to modeled estimated reporting rates. Further, our results are somewhat robust to under or overestimating reporting rate if hunter honesty is constant through time, under different management restrictions, and with population size. Consequently, we *post-hoc* examined sampled reports that could not be verified against harvest regulations (i.e., season length, bag limit), time, and Wellington Region population index. Results suggested no temporal, regulation-based, or density-dependent pattern in false or misreported bands (Fig. S5). However, hunter surveys would benefit from cross-checking hunter-reported bands with the recovery records and conducting follow up surveys with hunters that reported a band missing from the database.

Season regulations and harvest did not affect annual survival of mallards and grey ducks in our study contrary to the predictions of Barker et al. (1991) who reported harvest rates were additive to annual mortality of grey ducks banded in the Auckland-Waikato Region (1957–1974) when season regulations were constant. The inconsistency in findings could be due to the lower survival rate of grey ducks compared with mallards (Williams and Basse 2006). In our study, mallards predominated; about 14% of the birds were likely grey ducks or grey duck-mallard hybrids (M. B. McDougall, unpublished data).

We found, however, hunter effort explained changes in survival better than any of the other competing models; as hours hunting mallards and grey ducks increased, survival decreased. Previous studies have reported that human disturbance, including hunting (Szymanski et al. 2013), can make food functionally unavailable to waterfowl and increase energy expenditure through changes in habitat use and behavior (e.g., increased time in flight, nocturnal feeding; Frederick et al. 1987, Bélanger and Bédard 1990, Pease et al. 2005). In turn, disturbance may affect waterfowl body condition (Korschgen and Dalgren 1992, Bechet et al. 2004, Dooley et al. 2010) and population dynamics (Madsen 1995, Fox and Madsen 1997, Zimmer et al. 2010). Zimmer et al (2010) reported experimentally disturbed mallards fed less often and lost significantly more mass than undisturbed mallards. Moon and Haukos (2006) evaluated the effects of hunting on survival of northern pintails (*Anas acuta*) wintering in Texas and reported survival was associated with body condition and that movements increased drastically during the hunting season as a result of disturbance. They postulated that movement due to disturbance may lower body mass, which would decrease the likelihood of survival. Furthermore, Madsen (1995) reported that pink-footed geese (*Anser brachyrhynchus*) in Norway subjected to frequent disturbance prior to breeding accumulated less fat pre-breeding and had lower reproductive success compared to geese using undisturbed fields pre-breeding. The hunting season ends just before the mallard breeding season in NZ, which may exacerbate the effects of disturbance on body condition and subsequent survival and productivity, especially for females.

The effect of hunter effort on survival may also be mediated through the correlation between hunter effort and population size ($r = 0.65$). If hunter effort is a proxy for population size, then our results suggest survival decreases as population size increases. McDougall (2012), in a more restricted study of the same Eastern Region population, randomly partitioned banded birds into 2 groups similar to Nichols and Hines (1983); 1 group to estimate population size using the

Lincoln estimator (Alisauskas et al. 2013) and the other to estimate survival. He found post-harvest juvenile survival decreased with increasing estimates of population size. Post-harvest adult survival, however, showed signs that survival remained static at lower population levels but decreased when the population exceeded 250,000, which is consistent with our results suggesting increased survival for adult and juvenile females when populations were low (Fig. 7).

Environmental factors outside of those examined in our study also likely affect survival. For example, habitat loss and land-use change throughout our study period have been extensive (Walker et al. 2006), and likely influenced resource availability and predator communities through time, which in turn may affect waterfowl survival. Admittedly, our climate variables were coarse and based on only 1 regional weather station that may not represent the full heterogeneity in climactic patterns through time and space. Future examinations would benefit from examining how land-use change has interacted with harvest to influence population dynamics of mallards and grey ducks in NZ.

Our results are the first step toward implementing AHM in the Eastern Region in NZ, which requires the ability to predict harvest rates, and changes in survival, recruitment, and movement rates from a prescribed set of regulations to predict effects of anticipated harvest (Cooch et al. 2014). Our models could be integrated to predict the effect of harvest on population dynamics based on past management actions, and band recoveries from monitoring programs can provide estimates of population size, harvest rate, and annual survival to populate AHM models and determine the system state (e.g., population size; Cooch et al. 2014). However, managers must still define specific management objectives and the optimal action under each system state. Further, studies examining recruitment and movement rates of mallards and grey ducks are needed to inform mortality hypotheses and set baseline population thresholds for a comprehensive AHM framework.

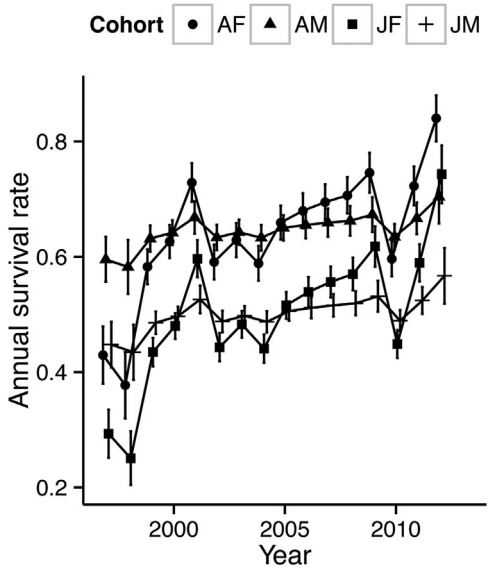

Figure 7. Adult female (AF), adult male (AM), juvenile female (JF), and juvenile male (JM) survival rates ($\bar{x} \pm 85\%$ CI) of mallards and grey ducks banded in the Eastern Fish and Game Region, New Zealand, 1997–2012.

Our study identified several additional knowledge gaps and avenues of future research. Our results suggest hunter effort, but not total harvest, affected annual survival and because the hunting season ends as breeding begins, hunting-related disturbance may also negatively affect breeding propensity, disrupt pair bonds, and lower reproductive output. However, we were unable to parse out the relative contributions of population size and hunter effort on survival (i.e., density dependence or disturbance, respectively) and this topic warrants further investigation. Second, given that reporting rate influences population estimates in the Eastern Region, it is important to obtain a reasonable annual estimate of reporting rate or an independent estimate of population size. Reward bands, field evaluations, or telemetry studies could be used to validate reporting rates or abundance estimates. Third, we observed a decline in hunter effort, but not participation, through time. Given the importance of license holders to funding habitat creation and management, this decrease warrants continued monitoring.

MANAGEMENT IMPLICATIONS

Condensed hunter effort and success at the beginning of the season, and non-compliance make it difficult to constrain harvest using season length regulations. Because 52–74% of harvest occurs by the end of the first 2 weeks (3 weekends), reducing season length to <31 days may only marginally affect total harvest unless the season is reduced to about 16 days. However, given the consistent behavior of Eastern Region hunters across the season, reducing 15 bird bag limits to 5 birds/day should reduce harvest by 25%; further reducing bag limits to <2 birds/day should decrease harvest by 50% (Fig. 4). These suggestions, however, are outside of the regulations used in this study and hunter behavior and patterns of effort may change as regulation constraint increases. Up to 13% of reported harvest during our study was illegal. Communicating and enforcing annual regulations with waterfowl hunters may improve the effectiveness of season length and bag limits on harvest management, but at the very least our results can be used to adjust harvest goals for illegal take during and after the hunting season.

ACKNOWLEDGMENTS

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LITERATURE CITED

Alisauskas, R. T., T. W. Arnold, J. O. Leafloor, D. L. Otis, and J. S. Sedinger. 2013. Lincoln estimates of mallard (*Anas platyrhynchos*) abundance in North America. Ecology and Evolution 4:132–143.

Anderson, D. R. 1975. Optimal exploitation strategies for an animal population in a Markovian environment: a theory and an example. Ecology 56:1281–1297.

Anderson, D. R., and K. P. Burnham. 1976. Population ecology of the mallard. VI. The effect of exploitation on survival. U.S. Fish and Wildlife Service Resource Publication 128, Washington, D.C., USA.

Anderson, D. R., W. A. Link, D. H. Johnson, and K. P. Burnham. 2001. Suggestions for presenting the results of data analyses. Journal of Wildlife Management 65:373–378.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74: 1175–1178.

Balham, R. W., and K. H. Miers. 1959. Mortality and survival of grey and mallard ducks in banded in New Zealand. New Zealand Department of Internal Affairs, Wellington, New Zealand.

Barker, R. J. 1991. Nonresponse bias in New Zealand waterfowl harvest surveys. Journal of Wildlife Management 55:126–131.

Barker, R. J., J. E. Hines, and J. D. Nichols. 1991. Effect of hunting on annual survival of grey ducks in New Zealand. Journal of Wildlife Management 55:260–265.

Barker, R. J., and D. I. MacKenzie. 1999. National game hunter survey review. Department of Maths and Statistics, University of Otago, Dunedin, New Zealand.

Bechet, A., J. F. Giroux, and G. Gauthier. 2004. The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese. Journal of Applied Ecology 41:689–700.

Bélanger, L., and J. Bédard. 1990. Energetic cost of man-induced disturbance to staging snow geese. Journal of Wildlife Management 54: 36–41.

Brocklesby, J., K. Shaw, and S. Hewitt. 1995. Summary report: attitudes towards hunting and fishing among licence holders. MRL Research Group, Wellington, New Zealand.

Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical inference from band recovery data—a handbook. U.S. Fish and Wildlife Service Resource Publication 131, Washington, D.C., USA.

Burnham, K. P. 1993. A theory for combined analysis of ring recovery and recapture data. Pages 199–213 *in* J. D. Lebreton and P. M. North, editors. Marked individuals in the study of bird populations. Birkhauser Verlag, Basel, Switzerland.

Burnham, K. P., and D. R. Anderson. 1984. Tests of compensatory vs. additive hypotheses of mortality in mallards. Ecology 65:105–112.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Caithness, T. 1982. Exploitation of waterfowl in New Zealand. New Zealand Journal of Ecology 5:155–158.

Caithness, T., M. Williams, and J. D. Nichols. 1991. Survival and band recovery rates of sympatric grey ducks and mallards in New Zealand. Journal of Wildlife Management 55:111–118.

Cooch, E., and G. C. White. 2006. Program MARK: a gentle introduction. http://www.phidot.org/software/mark/docs/book. Accessed 1 Sep 2009.

Cooch, E. G., M. Guillemain, G. S. Boomer, J.-D. Lebreton, and J. D. Nichols. 2014. The effects of harvest on waterfowl populations. Wildfowl Special Issue 4:220–276.

Crissey, W. F. 1969. Prairie potholes from a continental viewpoint. Pages 161–171 *in* Saskatoon wetlands seminar. Canadian Wildlife Service Report, Ottawa, Canada.

Dooley, J. L., T. A. Sanders, and P. F. Doherty. 2010. Mallard response to experimental walk-in and shooting disturbance. Journal of Wildlife Management 74:1815–1824.

Dzubin, A. 1969. Comments on carrying capacity of small ponds for ducks and possible effects of density on mallard production. Pages 138–160 *in* Saskatoon Wetlands Seminar. Canadian Wildlife Service Report, Ottawa, Canada.

Fox, A., and J. Madsen. 1997. Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. Journal of Applied Ecology 34:1–13.

Francis, C. M., J. R. Sauer, and J. R. Serie. 1998. Effect of restrictive harvest regulations on survival and recovery rates of American black ducks. Journal of Wildlife Management 62:1544–1557.

Frederick, R. B., W. R. Clark, and E. E. Klaas. 1987. Behavior, energetics, and management of refuging waterfowl: a simulation model. Wildlife Monographs 96:3–35.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–472.

Hooten, M., and N. Hobbs. 2015. A guide to Bayesian model selection for ecologists. Ecological Monographs 85:3–28.

Howerter, D. W., M. G. Anderson, J. H. Devries, B. L. Joynt, L. M. Armstrong, R. B. Emery, and T. W. Arnold. 2014. Variation in mallard vital rates in Canadian Aspen Parklands: The Prairie Habitat Joint Venture assessment. Wildlife Monographs 188:1–37.

Irving, R. M., and S. M. Beadel. 1992. Botanical surveys and assessments of wildlife reserves in the Te Teko Ecological district. Department of Conservation, Rotorua, New Zealand.

Johnson, F. A., G. S. Boomer, B. K. Williams, J. D. Nichols, and D. J. Case. 2015. Multilevel learning in the adaptive management of waterfowl harvests: 20 years and counting. Wildlife Society Bulletin 39:9–19.

Johnson, F. A., and D. J. Case. 2000. Adaptive regulation of waterfowl harvests: lessons learned and prospects for the future. Transactions of the 65th North American Wildlife and Natural Resources Conference, Rosemont, Illinois, USA.

Korschgen, C. E., and R. B. Dalgren. 1992. Human disturbances of waterfowl: causes, effects, and management handbook. U.S. Fish and Wildlife Service Leaflet 13.2.15.

Laud, P. W. 2013. Bayesian model selection. Pages 285–299 *in* J. P. Klein, H. C. Van Houwelingen, J. G. Ibrahim, and T. H. Scheike, editors. Handbook of survival analysis. CRC Press, Boca Raton, Florida, USA.

Leathwick, J., G. Wilson, D. Rutledge, P. Wardle, F. Morgan, K. Johnston, M. McLeod, and R. Kirkpatrick. 2003. Land environments of New Zealand. David Bateman Ltd., Auckland, New Zealand.

Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing 10:325–337.

Madsen, J. 1995. Impacts of disturbance on migratory waterfowl. Ibis 137: S67–S74.

Marchant, S., and P. J. Higgins. 1991. Handbook of Australian, New Zealand, and Antarctic birds, volume 1 ratites to ducks. Oxford University Press, Oxford, England.

Martin, E. M., and S. M. Carney. 1977. Population ecology of the mallard. IV. A review of duck hunting regulations, activity, and success, with special reference to the mallard. U.S. Fish and Wildlife Service Resource Publication 130, Washington, D.C., USA.

McDougall, M. 2012. Towards adaptive management of parera and mallard duck in New Zealand. Thesis, Massey, Palmerston North, New Zealand.

McDowall, R. M. 1994. Game keepers for the nation, the story of New Zealand's acclimatisation societies 1861–1990. Canterbury University Press, Christchurch, New Zealand.

Melville, D. S. 2011. New Zealand National Bird Banding Scheme. Bird Bander's Manual. Department of Conservation, Wellington, New Zealand

Miller, C., and J. Vaske. 2003. Individual and situational influences on declining hunter effort in Illinois. Human Dimensions of Wildlife 8:263–276.

Moon, J. A., and D. A. Haukos. 2006. Survival of female northern pintails wintering in the Playa Lakes Region of northwestern Texas. Journal of Wildlife Management 70:777–783.

Nichols, J., and F. Johnson. 1996. The management of hunting of Anatidae. Gibier Faune Sauvage 13:977–989.

Nichols, J. D. 2005. Modern open-population capture-recapture models. Princeton University Press, New Jersey, USA.

Nichols, J. D., and J. E. Hines. 1983. The relationship between harvest and survival rates of mallards: a straightforward approach with partitioned data sets. Journal of Wildlife Management 47:334–348.

Nichols, J. D., R. E. Reynolds, R. J. Blohm, R. E. Trost, J. E. Hines, and J. P. Bladen. 1995. Geographic variation in band reporting rates for mallards based on reward banding. Journal of Wildlife Management 59:697–708.

Nichols, J. D., M. Williams, and T. Caithness. 1990. Survival and band recovery rates of mallards in New Zealand. Journal of Wildlife Management 54:629–636.

National Institute of Water and Atmospheric Research. 2013. CliFlo: NIWA's national climate database on the web. National Institute of Water and Atmospheric Research Ltd, Auckland, New Zealand.

Otis, D. L. 2004. Mallard harvest distributions in the Atlantic and Mississippi Flyways during periods of restrictive and liberal hunting regulations. Journal of Wildlife Management 68:351–359.

Palmer, C., and E. Whitfield. 2009. Fish and Game New Zealand lapsed licence holder pilot project in Nelson/Marlborough and Wellington. Fish and Game, Kaiteriteri, New Zealand.

Pease, M. L., R. K. Rose, and M. J. Butler. 2005. Effects of human disturbances on the behavior of wintering ducks. Wildlife Society Bulletin 33:103–112.
Pollock, K. H., K. Tsai, and J. M. Hoenig. 1994. Band return models: use of solicited bands and separation of hunting and natural mortality. Journal of Wildlife Management 58:193–198.
R Development Core Team. 2015. R: a language and environment for statistical computing, reference index version 2.15.2. R Foundation for Statistical Computing, Vienna, Austria.
Reinecke, K. J., C. W. Shaiffer, and D. Don. 1992. Band reporting rates of mallards in the Mississippi Alluvial Valley. Journal of Wildlife Management 56:526–531.
Rhymer, J. M., and D. Simberloff. 1996. Extinction by hybridization and introgression. Annual Review of Ecology and Systematics 27:83–109.
Rhymer, J. M., M. J. Williams, and M. J. Braun. 1994. Mitochondrial analysis of gene flow between New Zealand mallards (*Anas platyrhynchos*) and grey ducks (*A. superciliosa*). Auk 111:970–978.
Schroeder, S. A., D. C. Fulton, J. S. Lawrence, and S. D. Cordts. 2014. Legitimization of regulatory norms: waterfowl hunter acceptance of changing duck bag limits. Human Dimensions of Wildlife 19:234–252.
Seber, G. 1970. Estimating time-specific survival and reporting rates for adult birds from band returns. Biometrika 57:313–318.
Sedinger, J. S., and E. A. Rexstad. 1994. Do restrictive harvest regulations result in higher survival rates in mallards? A comment. Journal of Wildlife Management 58:571–577.
Smith, G. W., and R. E. Reynolds. 1994. Hunting and mallard survival: a reply. Journal of Wildlife Management 58:578–581.
Stafford, J. D., and T. P. Aaron. 2007. Survival of radio-marked mallard ducklings in South Dakota. Wilson Journal of Ornithology 119:585–591.
Stafford, J. D., A. T. Pearse, C. S. Hine, A. P. Yetter, and M. M. Horath. 2010. Factors associated with hunter success for ducks on state-owned lands in Illinois, USA. Wildlife Biology 16:113–122.
Strickland, M. D., H. J. Harju, K. R. McCaffery, H. W. Miller, L. M. Smith, and R. J. Stroll. 1996. Harvest management. Fifth edition, revised. The Wildlife Society, Bethesda, Maryland, USA.
Szymanski, M. L., M. A. Johnson, and M. Grovijahn. 2013. Effects of hunting pressure and collection method bias on body mass of drake mallards. Journal of Wildlife Management 77:235–242.
Taber, R. D. 1971. Sustained yield management. Third edition. The Wildlife Society, Washington, D.C., USA.
Walker, S., R. Price, D. Rutledge, R. T. Stephens, and W. G. Lee. 2006. Recent loss of indigenous cover in New Zealand. New Zealand Journal of Ecology 30:169–177.
White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–138.
White, G. C., K. P. Burnham, and D. R. Anderson. 2001. Advanced features of program MARK. Pages 368–377 *in* Proceedings of the Second International Wildlife Management Congress. Wildlife, Land, and People: Priorities for the 21st Century. The Wildlife Society, Bethesda, Maryland, USA.
Williams, M. 1981. The duckshooter's bag. The Wetland Press, Wellington, New Zealand.
Williams, M. 1999. An assessment of grey duck *Anas superciliosa* X mallard *A. platyrhynchos* hybridisation. Department of Conservation, Wellington, New Zealand.
Williams, M., and B. Basse. 2006. Indigenous gray ducks, *Anas superciliosa*, and introduced mallards, *A. platyrhynchos*, in New Zealand: processes and outcome of a deliberate encounter. Acta Zoologica Sinica 52(Supplement):579–582.
Wright, V. L. 1978. Causes and effects of biases on waterfowl harvest estimates. Journal of Wildlife Management 42:251–262.
Zimmer, C., M. Boos, O. Petit, and J. P. Robin. 2010. Body mass variations in disturbed mallards *Anas platyrhynchos* fit to the mass-dependent starvation-predation risk trade-off. Journal of Avian Biology 41:637–644.

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