Survival estimates, mortality patterns, and population growth of Fennoscandian mallards *Anas platyrhynchos*

Gunnar Gunnarsson[1,2,*], Johan Elmberg[1], Lisa Dessborn[1,2], Niclas Jonzén[3], Hannu Pöysä[4] & Jari Valkama[5]

[1] *Aquatic Biology and Chemistry Group, Kristianstad University, SE-291 88 Kristianstad, Sweden (*e-mail: gunnar.gunnarsson@hkr.se)*
[2] *Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden*
[3] *Department of Theoretical Ecology, Lund University, SE-223 62 Lund, Sweden*
[4] *Finnish Game and Fisheries Research Institute, Joensuu Game and Fisheries Research, Yliopistokatu 6, FI-80100 Joensuu, Finland*
[5] *Finnish Museum of Natural History, FI-00014 University of Helsinki, Finland*

Long-term mallard capture–recapture data from Sweden and Finland were analyzed to describe temporal mortality patterns and reasons. We used program MARK and Seber models to estimate annual survival (S) and recovery (r) rates. Survival rates were used in a Monte Carlo simulation to evaluate the correspondence between observed and predicted annual population sizes of a Finnish sub-population. About 90% of recovered birds died from hunting. Most recoveries were from the hunting season, and more males than females were shot. Predation was the most common cause of natural mortality. Finnish capture–recapture data fitted best the global model in which survival and recovery vary with age and sex. Annual survival and recovery rates for adult and juvenile males and females were overlapping, ranging from 0.46 to 0.90 (survival) and 0.07 to 0.17 (recovery), whereas pulli had lower survival rates (0.21–0.42). Pulli that were successfully sexed at the time of ringing had higher recovery rates (female pulli: 0.23; male pulli: 0.32) than juveniles and adults. Density-dependent fledgling production was detected in the Finnish sub-population and was accounted for in the Monte Carlo simulation, which estimated predicted breeding population size quite well, although one of the observed annual values (2003) fell outside the 95% confidence limits.

Introduction

Knowledge about vital rates, limitation, and regulation of populations is essential for management as well as for basic understanding of long-term dynamics. This is especially true for waterfowl, which are managed for conservation, hunting as well as for wetland ecosystem function (Batt *et al*. 1992, Nichols *et al*. 1995). In addition, ducks are the main natural vectors for

avian influenza (Olsen *et al.* 2006), calling for more baseline information about mortality patterns in nature.

The mallard, *Anas platyrhynchos*, is one of the most widespread and numerous waterfowl in the Holarctic. It is an important quarry species in many countries, and it is thus likely that hunting significantly affects mortality rates of migrating and wintering populations. The actual population level effects of variation in hunting mortality depend a great deal on a species' capacity to compensate by increased per capita reproductive output (i.e. compensatory natality; Boyce *et al.* 1999, Williams *et al.* 2002), which by definition involves density dependence (e.g. Sheaffer 1998). It has been argued that hunting mortality is compensatory and hence of no crucial importance to mallard population growth (Anderson & Burnham 1976, Rogers *et al.* 1979), but more recently Smith and Reynolds (1992) and Pöysä *et al.* (2004) have suggested that hunting mortality may have changed from being compensatory to being additive.

Robust knowledge about mortality and productivity patterns is a prerequisite for successful and sustainable management of populations, particularly so for programs of adaptive management (Nichols *et al.* 1995, Williams *et al.* 2002). Mallard survival rates have been presented in a number of North American studies, of which many demonstrate sex, age and year effects (Blohm *et al.* 1987, Nichols *et al.* 1987, Reynolds *et al.* 1995, Arnold & Clark 1996, Giudice 2003, Lake *et al.* 2006; for related species *see* e.g. Conroy & Eberhardt 1983, Johnson *et al.* 1992, Chu *et al.* 1995, Dufour & Clark 2002, Nicolai *et al.* 2005). Vital rates have been studied in European ducks, too. For example, age-specific survival in females of the northern shoveler *A. clypeata*, the common pochard *Aythya ferina* and the tufted duck *Aythya fuligula* were investigated in Latvia (Blums *et al.* 1996), and age- and sex-specific survival in Eurasian teal *Anas crecca* was studied in Britain (Gitay *et al.* 1990). Survival rates in European mallards have been reported in national bird ringing recovery atlases (e.g. Fransson & Pettersson 2001, Wernham *et al.* 2002, Bakken *et al.* 2003) as well as in scientific papers (Höhn 1948, Olsson 1960, Bentz 1985), but none of those were based on the more powerful and rigorous modern techniques for analysing ringing data (e.g. Brownie *et al.* 1985, Lebreton *et al.* 1992, White & Burnham 1999, Burnham & Anderson 2002).

Although there are a number of well-designed and influential North American studies on vital rates in waterfowl, including the mallard, these cannot be used uncritically for management in Europe. Many fundamental conditions differ between the continents, natural as well as those related to monitoring and legislation. In other words, we lack accurate vital rate data for European mallards, as is also true for estimates of breeding population size and harvest statistics (Elmberg *et al.* 2006). Consequently, based on present knowledge it is impossible to understand and explain population dynamics, let alone to forecast population growth and sustainable harvest levels of one of Europe's most important game species.

To address this deficiency, we here use ringing and dead-recovery data from Finland and Sweden, with emphasis on temporal annual variation and causes of death. Based on Finnish ringing data from 1973–2005, we also estimate survival and recovery rates by model fitting in program MARK. Our survival estimates were further used in a simulation of population growth using data from a Finnish sub-population to represent Fennoscandian mallards.

Materials and methods

Ringing data from Sweden and Finland

We used nationwide data on mallards ringed in Sweden (years 1919–2005) and Finland (1913–2005), provided by the national ringing centres in these countries (for geographical distribution of marked birds, *see* Table 1). Most Finnish mallards (79.3%) were ringed in May–August, whereas the great majority (82.1%) of Swedish birds were marked in June–December. Swedish data concern encountered birds only, i.e. data were not available for ringed mallards that were not encountered again. For Finnish mallards, complete capture–recapture data were available for the period 1973–2005 (Appendix), restricting us to the latter data set for the capture–recap-

ture analysis (*see* below). However, data from both countries and all years were used to get an overview of mortality patterns (by sex, age, month, and country). Dead-recovered (hereafter called 'recovered') mallards died either by natural causes or were killed by humans.

We strived to include only truly wild mallards with natural behaviour and migratory habits. A substantial part of the original data set was therefore not used; specifically we excluded birds that were (1) kept in captivity after marking and/or released more than 10 km from the ringing site, (2) held in captivity for more than 24 hours after capture, (3) in poor condition, (4) used in experiments, (5) of uncertain status at recapture (i.e. dead or alive), (6) recovered but with unknown time of death, (7) of uncertain encounter date, (8) encountered in mid-winter (December–March) in three urban park areas where mallards are regularly fed (Helsinki, Finland, 60°11´N, 24°53´/24°59´E; Turku, Finland, 60°26´N, 22°15´E; and Malmö, Sweden, 55°34´–55°37´N, 12°58´–13°02´E), (9) influenced by other factors which may have biased encounter probabilities (as denoted by the EURING exchange-code 2000; Speek *et al.* 2001). All of the above exclusion criteria were used for all analyses except for cause of death, in which criteria 6 and 7 were relaxed.

Capture–recapture analysis of Finnish mallards 1973–2005

In the analysis of survival and recovery we used mallards marked in Finland 1973–2005 divided into ten groups: adult females ($n = 146$), adult males ($n = 54$), juvenile females ($n = 133$), juvenile males ($n = 133$), unsexed juveniles ($n = 69$), female pulli ($n = 140$), male pulli ($n = 188$), unsexed pulli ($n = 1381$), unaged females ($n = 481$), and unaged males ($n = 374$) (Appendix). Subsequently, the classes 'unsexed adults' and 'unaged unsexed' were excluded due to low sample size (1 and 15, respectively). Mallards in their second calendar year or older were considered adult, whereas 'juveniles' were first-calendar-year birds. Birds without primaries were considered pulli, naturally excluding moulting adults.

We used program MARK (White & Burnham 1999) and the Seber modelling approach with dead recoveries only (Seber 1970). This approach includes survival (S_i) and recovery (r_i) parameters, where the r_i parameters represent the probability of individuals being recovered and reported (cf. e.g. Brownie parameterisation in Brownie *et al.* 1985). An encounter history with the LD ('Live–Dead') data format was constructed for each individual for 33 occasions (years), and the interval that survival and recoveries represent is, thus, from marking in year i to $i + 1$. Goodness of fit was tested using the bootstrap approach with 500 simulations of the most parameterised model with precisely estimated parameters only, and dividing the model deviance by the mean deviance from the bootstrap simulations. We consequently estimated the variance inflation factor ($\hat{c}$) to control for over-dispersion. From the global model (*see* Table 2) we systematically ran simplified and biologically relevant alternative models (Doherty *et al.* 2002), and ranked them using the quasi-likelihood Akaike's Information Criterion adjusted for low sample size (QAIC$_c$) (Akaike 1973, Burnham & Anderson 2002). The group effect consists of both *sex* and *age* in different combinations, and these categories were subsequently split from the "group" variable to see if their separate effects resulted in models with higher rank. Annual variation

Table 1. Latitudinal distribution of marking sites of encountered Finnish and Swedish mallards. Percentage of the total is given in parentheses.

Latitude (°N)	Sweden	Finland
68	1 (< 0.1)	1 (0.1)
67	4 (0.1)	0 (0)
66	4 (0.1)	0 (0)
65	7 (0.2)	56 (3.2)
64	2 (0.1)	19 (1.1)
63	29 (0.8)	67 (3.8)
62	8 (0.2)	85 (4.9)
61	59 (1.6)	363 (20.7)
60	54 (1.5)	1149 (65.7)
59	570 (15.4)	10 (0.6)
58	229 (6.2)	–
57	226 (6.1)	–
56	1812 (49.1)	–
55	686 (18.6)	–
Total	3691 (100)	1750 (100)

in survival and recovery parameters were not considered because of deficient data for several groups in some years (*see* Appendix). Models were considered to differ in fit when the difference in QAIC_c was greater than or equal to 2.00 (Burnham & Anderson 2002). Estimates for real function parameters based on the highest ranked model are presented for survival and recovery.

Population growth simulation

Population growth was simulated using data from pair and brood surveys in 1997–2006 organised by the Finnish Game and Fisheries Research Institute (e.g. Pöysä *et al*. 1993, Pöysä 1998). The surveys used in the present study were carried out by two persons, one in southern Finland (mean latitude of 46 sites: 62°12´N) and the other in northern Finland (mean latitude of 51 sites: 67°12´N). Both survey programs were based on a standardised waterfowl point count method (Koskimies & Väisänen 1991) and the same sites were used in all years. Breeding pair count data were used to estimate the size of the breeding population, which is thus equivalent to the number of breeding females. In the brood counts the number of ducklings in each brood

was recorded if possible, as was also brood age using the seven age classes of Pirkola and Högmander (1974): Ia–c, IIa–c, III; i.e. a combination of Gollop and Marshall (1954) and Linkola (1962). As duckling mortality is very low in broods older than three weeks (Hill *et al*. 1987, Orthmeyer & Ball 1990), we used the number of ducklings in age classes IIa–c and III as an index of fledgling success. For age class I broods, we used the observed number only if it was lower than the mean for age class II–III ducklings in that area and year; otherwise we used the mean size of age class II–III broods. The latter value was also used when the number of ducklings in a brood could not be firmly established. Because ringing data originated from the entire country (*see* above), we pooled population data from the two study areas (called 'Finnish sub-population').

We simulated population growth in MATLAB (The MathWorks 2000) using a model describing the dynamics of the number of breeding females, defined as

$$N_{t+1} = s_a N_t + s_p a N_t e^{-bN_t}, \qquad (1)$$

where S_a and S_p are the annual survival rates of adult and pulli females, respectively (*see*

Table 2. Model output from program MARK including survival (*S*) and recovery (*r*) parameters for mallards ringed in Finland 1973–2005 (*N* = 3099). *Sex* is either female, male, or unknown, and *age* is either pullus, juvenile, adult, or unknown but fledged. The global model is #1 and was used to estimate the variance inflation factor ($\hat{c}$).

Model	QAIC_c[a]	ΔQAIC_c[b]	w_i[c]	K[d]	Deviance[e]
1. $S_{(sex+age)}$ $r_{(sex+age)}$	2318.42	0.00	1.00	20	667.89
2. $S_{(sex+age)}$ $r_{(sex)}$	2342.39	23.98	0.00	13	706.02
3. $S_{(sex)}$ $r_{(sex+age)}$	2361.37	42.95	0.00	13	724.99
4. $S_{(age)}$ $r_{(.)}$	2394.37	75.95	0.00	5	774.09
5. $S_{(sex+age)}$ $r_{(.)}$	2394.49	76.07	0.00	11	762.14
6. $S_{(age)}$ $r_{(age)}$	2399.11	80.69	0.00	8	772.80
7. $S_{(sex+age)}$ $r_{(age)}$	2399.55	81.13	0.00	14	761.15
8. $S_{(.)}$ $r_{(sex+age)}$	2401.69	83.27	0.00	11	769.35
9. $S_{(.)}$ $r_{(sex)}$	2435.86	117.44	0.00	4	817.59
10. $S_{(sex)}$ $r_{(.)}$	2445.25	126.83	0.00	4	826.98
11. $S_{(.)}$ $r_{(.)}$	2482.49	164.07	0.00	2	868.23
12. $S_{(.)}$ $r_{(age)}$	2486.85	168.44	0.00	5	866.57

[a] quasi-likelihood Akaike's Information Criterion adjusted for low sample size.

[b] difference between QAIC_c of the current model and the minimum QAIC_c value.

[c] normalised Akaike weight.

[d] number of parameters.

[e] difference in –2log(likelihood) of the current model and –2log(likelihood) of the saturated model (i.e. the model containing as many parameters as the sample size).

Table 3), *a* is the maximum number of female fledglings per pair (assuming a 50/50 sex ratio among fledglings) and *b* is the strength of density dependence. Other recruitment functions might also be relevant, but our results turned out to be robust to alternative model formulations. We wanted to use a simple model likely to explain most of the variation, hence avoiding models including too many imprecisely estimated parameters (e.g. breeding and re-nesting probabilities that also may be important for population growth). We estimated *a* and *b* by fitting the recruitment function to data assuming a log-normal error structure (Hilborn & Mangel 1997). To evaluate the plausibility of predicted annual population sizes, we generated 10 000 time series using Eq. 1 and sampling from the survival parameter distributions estimated from the capture–recapture analysis. These Monte Carlo data were compared with the observed annual population size.

Results

General patterns of mortality and survival

After relaxing exclusion criteria 6 and 7 (*see* Material and methods), 92.4% (*n* = 3411) of all encountered Swedish mallards (*n* = 3691) were found dead. The proportion of live encounters (recaptures or re-sightings) was hence 7.6% (*n* = 280). The ratio between live and dead encounters was quite different for Finnish mallards, though; 41.7% (*n* = 730) was recaptured or re-sighted alive, whereas 58.3% (*n* = 1020) was reported dead.

Among recovered mallards ringed in Sweden, mortality was caused by humans in 97.0% of the cases; hence 3.0% died naturally. This ratio was rather consistent in terms of sex (females: 96.8:3.2; males: 97.1:2.9; unknown sex: 96.7:3.3). Human-induced mortality was due to hunting (92.8%; *n* = 3166), traffic or other collisions (2.5%; *n* = 86), oil spills or other types of pollution (0.8%; *n* = 26), and other causes (unintentional trapping, tangled in man-made objects etc., 0.9%, *n* = 29). Predation was the most common type of natural mortality (1.8%; *n* = 63), followed by disease (0.7%; *n* = 25), and

other causes (drowned, tangled in natural objects etc., 0.5%; *n* = 16).

Based on ringing recovery data, the mortality pattern in Finnish mallards was similar; 4.8% (*n* = 49) died from natural causes whereas 95.2% (*n* = 971) died as a result of human activities. In contrast to the Swedish recoveries, more males than females were killed by man; females: 89.7:10.3; males: 94.2:5.8; unknown sex: 98.3:1.7 (cf. ratio for Swedish birds above). 86.3% (*n* = 880) of all recovered Finnish mallards ended up in hunters' bags, 7.4% (*n* = 75) died in traffic or other collisions, 1.1% (*n* = 11) was killed by oil or other pollutants, and 0.5% (*n* = 5) died from other human-related causes (*see* above for Swedish mallards). Natural mortality was due to predation (4.3%, *n* = 44), disease (0.3%, *n* = 3), and other causes (see above for Swedish birds) (0.2%, *n* = 2).

The oldest Swedish mallard was a male ringed in 1970 as 2+cy (i.e. in its second calendar year or older); it was found dead (caused by pollution, not oil) in 1994 being at least 25 years old (26+cy). The oldest Finnish mallard was a female ringed in 1978, being at least 19 years old (20+cy) when recovered in 1997 after being killed by an eagle owl *Bubo bubo*. However, the mean age of recovered mallards was much lower, only 1.44 (SD = 2.00) years in Swedish and 1.19 (SD = 1.96) years in Finnish birds. Combining data from both countries produced a mean recovery age of 1.38 (SD = 2.00) years.
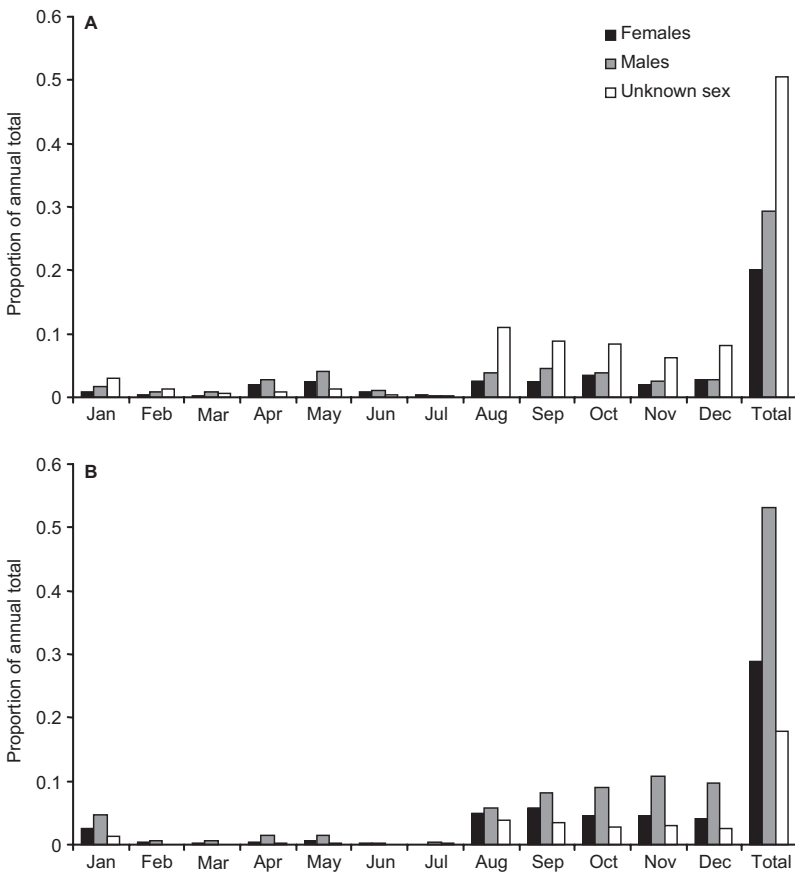
The age distribution pattern of recovered mallards was more or less the same for both countries (Fig. 1; 13+cy birds were excluded as

Table 3. Seber model estimates of annual survival and recovery with 95% confidence intervals for mallards marked in Finland 1973–2005.

Group	Survival rate	Recovery rate
Adult females	0.73 (0.52–0.87)	0.09 (0.05–0.16)
Adult males	0.90 (0.37–0.99)	0.12 (0.02–0.50)
Juvenile females	0.46 (0.24–0.69)	0.11 (0.06–0.19)
Juvenile males	0.75 (0.61–0.86)	0.17 (0.11–0.27)
Unsexed juveniles	0.71 (0.43–0.89)	0.07 (0.03–0.18)
Female pulli	0.27 (0.14–0.45)	0.23 (0.16–0.32)
Male pulli	0.42 (0.31–0.54)	0.32 (0.25–0.40)
Unsexed pulli	0.21 (0.14–0.31)	0.06 (0.05–0.08)
Unaged females	0.71 (0.61–0.79)	0.08 (0.06–0.12)
Unaged males	0.70 (0.62–0.78)	0.13 (0.10–0.17)
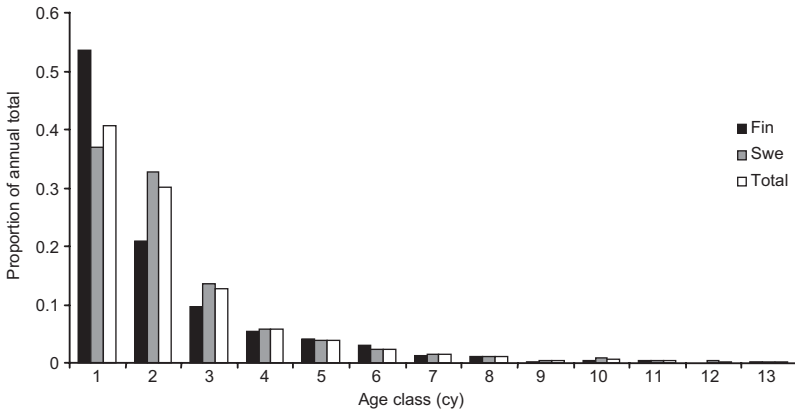
Fig. 1. Age class distribution (1st–13th calendar year (cy)) of recovered mallards ringed in Finland (*n* = 503) and Sweden (*n* = 1761).


Fig. 2. Monthly distribution of recovered mallard ringed in (**A**) Finland (*n* = 503), and (**B**) Sweden (*n* = 1761).

there were only two each from Sweden and Finland). However, more first-calendar-year birds were recovered in Finland than in Sweden and, consequently, more 2cy birds were recovered in Sweden than in Finland.

In a monthly analysis there was a general pattern of more males than females being recovered (paired *t*-test: Finland: $t_{11} = -3.93$, $p = 0.002$; Sweden: $t_{11} = -3.16$, $p = 0.009$; Fig. 2). There was no estimated bias in the number of ringed males and females since the complete capture–recapture data set from Finland 1973–2006 revealed no sex differences in the number of birds ringed per month (paired *t*-test: $t_{11} = 0.73$, $p = 0.484$).

Fig 3. Density-dependent fledgling production in mallards in the Finnish sub-population based on 10 years of data (linear regression: $t = 6.06$, $n = 10$, $p = 0.039$). The maximum number of female fledglings per breeding pair (a) and the strength of density dependence (b; i.e. the slope) in the linear function were $a = 2.5$ and $b = 0.021$.
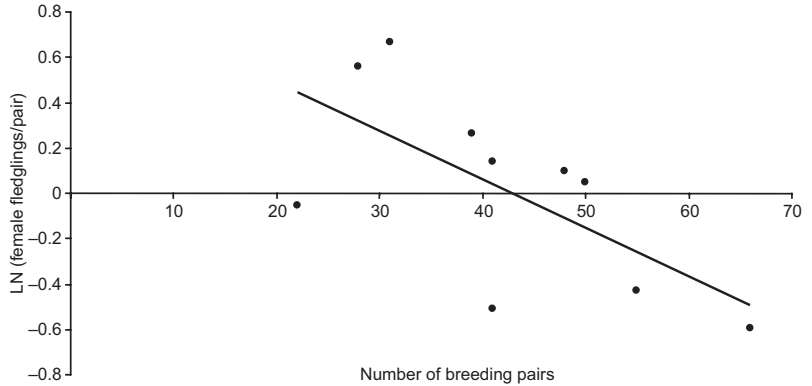
Capture-recapture analysis of Finnish mallards 1973–2005

After all exclusions based on the criteria listed in Material and methods, 3099 marked birds remained for the 10 groups of different sex and age (*see* Material and methods), of which 313 (10.1%) were later recovered (same year as ringing or later).

The most parameterised model, used for $\hat{c}$ estimation, was $S_{(sex+age)} \, r_{(sex+age)}$ (model #1 in Table 2). Over-dispersion was controlled for by adjusting $\hat{c}$ to 1.19, calculated as the deviance in this model (794.48) divided by the deviance in the simulated model (667.89).

The highest ranked model (#1 in Table 2) allows survival and recovery probabilities to vary by sex and age, and its model weight (w_i) of 1.00 compared with that of the second highest ranked model ($w_i = 0.00$; $\Delta QAIC_c = 23.98$) shows that the former is outstanding compared with all other models.

Because the group categorisation used included both sex and age in different combinations, we separated those effects in a final set of models, where the top model was re-assessed by adding either sex or age effects in separate models. These had much higher $QAIC_c$ values ($\Delta QAIC_c \geq 23.98$; *see* Table 2) compared with the former top model, and we therefore conclude that both sex and age are important to survival and recovery probabilities.

Adults and juveniles seem to have about the same survival (range 0.46–0.90) and recovery (range 0.07–0.17) probabilities, since the standard errors for the estimates were overlapping (Table 3). On the other hand, mallard pulli had lower survival rates (0.21–0.42) compared to juveniles and adults. Similarly, sexed pulli had higher recovery rates (female pulli: 0.23; male pulli: 0.32) than juveniles and adults (Table 3).
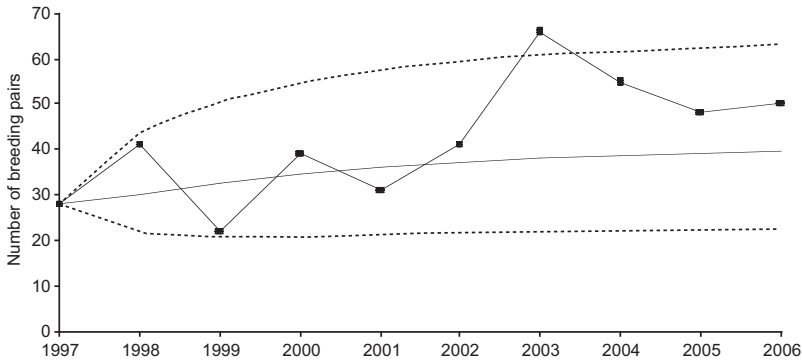
Population growth simulation

Production of female fledglings per pair (log-normally transformed values) was negatively correlated with breeding population size (Fig. 3); i.e. fledgling production was density-dependent. Consequently, estimates of maximum female fledglings per pair (a) and power of density dependence (b) were taken from the equation describing the linear relationship shown in Fig. 3 and were used for the Monte Carlo simulation. Plotting the annual estimates of observed breeding population size against the predicted ones from the Monte Carlo simulation resulted in an overall good estimation of the predicted annual population size even though observed data from one year (2003) fell outside the 95% confidence interval (Fig. 4).

Discussion

General patterns of mortality and survival

Bentz (1985) found that almost 90% of the recovered mallards marked in urban parks in southern Sweden were shot (cf. Fransson & Pettersson 2001). This corresponds very well with the hunting recovery rate of 86.3%–93.9% in our

Fig. 4. Simulated population growth (solid line) with 95% confidence limits (hatched) and observed annual population size (grey) of the Finnish subpopulation in 1997–2006.

data set. Studies elsewhere in Europe (Wernham *et al.* 2002) concur that hunting mortality is by far the most common cause of death, whereas North American data suggest more equal shares of natural *vs.* human-induced mortality (Baldassarre & Bolen 2006), or even imply that the former is higher than the latter (e.g. Bergan & Smith 1993).

There was a striking difference between Sweden and Finland in the proportion of mallards encountered live and dead. The Swedish pattern, with recoveries far exceeding recaptures and re-sightings, is well in line with other European studies (Wernham *et al.* 2002, Bakken *et al.* 2003). Since Swedish and Finnish mallards arguably belong to the same population, our diverging results are most likely due to differences in bird ringing and/or hunting practices between the two countries. Firstly, circumstances for the live encounters actually differ; 32.7% of the Finnish birds were recaptured by ringers, whereas 64.2% were re-sighted without recapture. Corresponding numbers for Swedish birds are 57.5% and 41.8%, respectively. Secondly, it may be that relatively more hunting occurs north of the main ringing areas in Finland (cf. Table 1). In Sweden on the other hand, most hunting occurs in the south, which is also where most birds are ringed.

In both countries, most recoveries were from August–December (Sweden 83.5% and Finland 73.7%; cf. Fig. 2; Bentz 1985), i.e. when there is still a large proportion of naive first calendar year birds in the population. These are also the main duck hunting months in Fennoscandia as well as in many other important wintering areas farther southwest. Broadly speaking, this type of temporal pattern is similar to that found in North American mallards; approximately 85% of the recoveries in Hickey (1952) were from the duck hunting season.

We found that more males than females were recovered, which is in concordance with earlier mallard studies (e.g. Bentz 1985, Soutiere 1989, Smith & Reynolds 1992, Johnson & Moore 1996, Giudice 2003). However, we are cautious about drawing any conclusions about naturally skewed sex ratios; many of the recovered birds were not sexed, neither in our data (Fig. 2) nor in other studies. In other words, a dominant proportion of the reported unsexed mallards may have been females. This caveat should be kept in mind also when judging the apparent higher proportion of males (*vs.* females) killed by man in the Finnish data. Even though this pattern is supported by earlier studies (*see* e.g. Batt *et al.* 1992), we can not conclude that more males than females are killed by man, because of the uncertainty created by many birds being unsexed. It is also important to realise that the above conclusions about mortality are based on recovery data, which is also true for most of the studies cited here. Such data may be biased by giving information about ringed birds that were later recovered, but not about those that were not encountered again. Recovery data thus may or may not tell the truth about mortality factors.

Capture–recapture analysis of Finnish mallards 1973–2005

According to the top model in Table 2, annual survival varies with both sex and age. However,

judging from the real function parameters in Table 3, there are no clear sex differences for either of the age groups since confidence intervals overlap. Still, despite some overlap between juvenile males and females, there is a tendency for females to have lower annual survival. This corroborates other studies on mallards and other ducks showing that females often have a lower survival rate than males (cf. table 14.1 in Johnson *et al*. 1992, Nicolai *et al*. 2005, Lake *et al*. 2006). We hypothesised that adult survival, too, should differ between sexes, and it was surprising that it did not. The most likely explanation is the low sample size for adult males (Appendix), leading to a very wide confidence interval for this group. In fact, in all age groups except for unaged birds, survival means are lower for females than males, and this pattern would probably have been clearer still with larger sample sizes.

Juveniles do not seem to have a different annual survival rate than adults (Table 3). Mallards of unknown age (juveniles or adult) did not differ from adults and juveniles either, implying that there is no distinct difference in survival between the two age classes. In this context it is important to mention that juveniles in our data set by definition are so for only about half a year (from being fledged in summer to 31 December), whereas an adult's year lasts from 1 January to 31 December. In other words, juveniles have a shorter 'reporting year', which may lead to biased higher annual survival rate. We expected lower survival in juveniles, as has been found in many previous studies (e.g. table 14.1 in Johnson *et al*. 1992). The story is definitely different for birds marked as pulli; it is well known that pre-fledgling ducklings have much higher mortality than any other age category (review in Batt *et al*. 1992). Our data confirm this, and especially unsexed pulli had low annual survival. The most likely explanation is that sexed pulli were older than unsexed (sex characteristics become more distinct as ducklings grow older); younger pulli have lower daily survival than older ones (Hill *et al*. 1987, Orthmeyer & Ball 1990, Rotella & Ratti 1992, Sargeant & Raveling 1992, Pietz *et al*. 2003).

The top model also suggests that there is variation in recovery rate due to sex and age group. As for survival above, there are no clear sex effects, even though female pulli and unaged females seem to have somewhat lower recovery rates (Table 3). Once again, we have to acknowledge that some groups comprise quite few ringed birds, which consequently will give very few recoveries (e.g. adult males; Appendix) and a low accuracy for survival and recovery estimates in these groups.

In general, most recoveries are due to hunting, and because most pulli die young of natural causes, they simply will not live long enough to become quarry, probably causing the low recovery rate in unsexed pulli (Table 3). On the contrary, pulli of known sex (i.e. generally older ones), have relatively high recovery rates. This is probably because they are naive and more likely than other age groups to become harvested.

There are many published estimates of annual survival in mallards, but data quality and analytical approaches differ. With this caveat in mind, annual survival rates reported here are rather high compared with previous Fennoscandian studies, some of which included many urban birds (cf. 0.30–0.44 in juveniles and 0.57–0.66 in adults; Koskimies 1956, Olsson 1960, Bentz 1985). The latter estimates were, however, not calculated with a capture-recapture approach according to Brownie *et al*. (1985) and true survival rates may have been underestimated. Yet, our use of such techniques should produce estimates comparable to those in similar North American studies. Acknowledging the differences in hunting pressure, guild composition, latitudinal provenance of marked birds, and predator communities between the continents, our estimates of annual survival are consistently higher than those reported from North America (Arnold & Clark 1996, Giudice 2003; cf. table 14.1 in Johnson *et al*. 1992). The present study explores capture–recapture data from birds largely emanating from the boreal and, interestingly, there is an indication of higher annual survival in boreal ducks in North America, too (Lake *et al*. 2006). The latter study did not include mallard, but it still indicates that there is a latitudinal effect on survival rate in waterfowl.

Finally we would like to point out that the Finnish data used for estimating survival and recovery probabilities were nationwide, and we

acknowledge that data heterogeneity (e.g. using different capture methods, birds marked in different months, etc.) may have affected the precision of the estimates.

Population growth simulation

Predicted annual population sizes fit quite well the observed, even though observed data from one year (2003) fell outside the 95% CI limits. We acknowledge that time-invariant survival estimates may be inappropriate to use, and to evaluate our data, a separate simulation in program MARK was performed. Here we entered different and hypothetical sample sizes, but we found that including annual variation for survival lowered the overall data fit (G. Gunnarsson *et al.* unpubl. data). As the detection probability of pairs and ducklings is not 100%, one might argue that the modelling results may be affected. We do not consider this being an important source of error, however; if any, it should be a constant systematic error because the same skilled persons surveyed the same sites every year using a standardized waterfowl point count method.

Fledgling production in the Finnish sub-populations was density-dependent (Fig. 3), which is a very interesting result in its own right, corroborating previous descriptive and experimental results from nemoral and boreal sites in Sweden (Elmberg 2003, Elmberg *et al.* 2005, Gunnarsson *et al.* 2006), but contradicting two descriptive Finnish studies (Pöysä 2001, Elmberg *et al.* 2003). The present study emphasises the importance of accounting for density dependence in population dynamics; population size predicted by us would certainly have been overestimated if not density dependence was included in the simulation.

Studying population processes is complex, and our assumption of a closed population is likely not true. In fact, this could explain why there was not a perfect fit between predicted and observed population sizes. Fennoscandian mallards may be part of a large-scale source-sink dynamics system, in which 'surplus mallards are exported' to other areas (cf. Pulliam & Danielson 1991, Amarasekare 2004). Moreover, density-dependent processes may operate in winter or early spring too, in which context it is important to acknowledge that many of the 'Fennoscandian' mallards in our data set may have been transient Baltic and Russian breeders on their way to wintering grounds farther southwest (cf. Fransson & Pettersson 2001, Wernham *et al.* 2002).

This is the first simulation of population growth in European mallards based on empirically derived estimates for survival and fledgling production. However, we acknowledge that there are still gaps in our understanding of the crucial population processes and that uncertainty remains in the estimates of the critical population parameters. Future research should focus on filling those gaps and improving the accuracy of data. In particular, use of larger data sets will probably demonstrate annual variation in survival rate. Finally, in order to be able to understand population dynamics of European mallards we also need to identify the factors that determine settlement patterns of pairs on the breeding grounds.

Acknowledgements

References

Akaike, H. 1973: Information theory and an extension of the maximum likelihood principle. — In: Petran, B. N. & Csáki, F. (eds.), *Proceedings of the 2nd international symposium on information theory*: 267–281. Akadémiai Kiadi, Budapest, Hungary.

Amarasekare, P. 2004: The role of density-dependent dispersal in source-sink dynamics. — *J. Theor. Biol.* 226: 159–168.

Anderson, D. R. & Burnham, K. P. 1976: Population ecology of the mallard. VI. The effect of exploitation on survival. — *U.S. Dep. Int. Fish Wildl. Ser. Res. Publ.* 128: 1–66.

Arnold, T. W. & Clark, R. B. 1996: Survival and philopatry of female dabbling ducks in southcentral Saskatchewan. — *J. Wildl. Manage.* 60: 560–568.

Bakken, V., Runde, O. & Tjørve, E. 2003: *Norwegian bird ringing atlas*. — Stavanger Museum, Stavanger.

Baldassarre, G. A. & Bolen, E. G. 2006: *Waterfowl ecology and management*, 2nd ed. — Krieger Publishing Company, Malabar.

Batt, B. D. J., Afton, A. D., Anderson, M. G., Ankney, C. D., Johnson, D. H., Kadlec, J. A. & Krapu, G. L. (eds.) 1992: *Ecology and management of breeding waterfowl*. — University of Minnesota Press, Minneapolis.

Bentz, P.-G. 1985: Studies on some urban mallard *Anas platyrhynchos* populations in Scandinavia. Part I: Causes of death, mortality and longevity among Malmö Mallards as shown by ringing recoveries. — *Fauna Norv. Ser. C* 8: 44–56.

Bergan, J. F. & Smith, L. M. 1993: Survival rates of female mallards wintering in the Playa Lakes region. — *J. Wildl. Manage.* 57: 570–577.

Blohm, R. J., Reynolds, R. E., Bladen, J. P., Nichols, J. D., Hines, J. E., Pollock, K. H. & Eberhardt, R. T. 1987: Mallard mortality rates on key breeding and wintering areas. — *Trans. N. Am. Wildl. Nat. Res. Conf.* 52: 246–257.

Blums, P., Mednis, A. & Bauga, I. 1996: Age-specific survival and philopatry in three species of European ducks: a long-term study. — *Condor* 98: 61–74.

Boyce, M. S., Sinclair, A. R. E. & White, G. C. 1999: Seasonal compensation of predation and harvesting. — *Oikos* 87: 419–426.

Brownie, C., Anderson, D. R., Burnham, K. P. & Robson, D. S. 1985: *Statistical inference from band recovery data — a handbook*, 2nd ed. — U.S. Fish and Wildlife Service, Resource Publication 156, Washington.

Burnham, K. P. & Anderson, D. R. 2002: *Model selection and multi-model inference: a practical information-theoretic approach*, 2nd ed. — Springer-Verlag, New York.

Chu, D. S., Nichols, J. D., Hestbeck, J. B. & Hines, J. E. 1995: Banding reference areas and survival rates of green-winged teal, 1950–89. — *J. Wildl. Manage.* 59: 487–498.

Conroy, M. J. & Eberhardt, R. T. 1983: Variation in survival and recovery rates of ring-necked ducks. — *J. Wildl. Manage.* 47: 127–137.

Doherty, P. F. Jr., Nichols, J. D., Tuatin, J., Voelzer, J. F., Smith, G. W., Benning, D. S., Bentley, V. R., Bidwell, J. K., Bollinger, K. S., Brazda, A. R., Buelna, E. K., Goldsberry, J. R., King, R. J., Roetker, F. H., Solberg, J. W., Thorpe, P. P. & Wortham, J. S. 2002: Sources of variation in breeding-ground fidelity of mallards (*Anas platyrhynchos*). — *Behav. Ecol.* 13: 543–550.

Dufour, K. W. & Clark, R. G. 2002: Differential survival of yearling and adult female mallards and its relation to breeding habitat conditions. — *Condor* 104: 297–308.

Elmberg, J. 2003. Density-dependent breeding success in mallards *Anas platyrhynchos* on a eutrophic lake. — *Wildl. Biol.* 9: 67–73.

Elmberg, J., Gunnarsson, G., Pöysä, H., Sjöberg, K. & Nummi, P. 2005: Within-season sequential density dependence regulates breeding success in mallards *Anas platyrhynchos*. — *Oikos* 108: 582–590.

Elmberg, J., Nummi, P., Pöysä, H. & Sjöberg, K. 2003: Breeding success of sympatric dabbling ducks in relation to population density and food resources. — *Oikos* 100: 333–341.

Elmberg, J., Nummi, P., Pöysä, H., Sjöberg, K., Gunnarsson, G., Clausen, P., Guillemain, M., Rodrigues, D. & Väänänen, V.-M. 2006: The scientific basis for a new and sustainable management of migratory European ducks. — *Wildl. Biol.* 12: 121–127.

Fransson, T. & Pettersson, J. 2001: *Svensk ringmärkningsatlas* [*Swedish bird ringing atlas*]. — Ljungföretagen Tryckeri AB, Örebro. [In Swedish with English summary].

Gitay, H., Fox, A. D. & Ridgill, S. C. 1990: Survival estimates of teal (*Anas crecca*) ringed at three stations in Britain. — *The Ring* 13: 45–58.

Giudice, J. H. 2003: Survival and recovery of Mallards and Gadwalls banded in eastern Washington, 1981–1998. — *J. Field Ornith.* 74: 1–11.

Gollop, J. B. & Marshall, W. H. 1954: *A guide to ageing duck broods in the field*. — Mississippi Flyway Council, Technical Section Report.

Gunnarsson, G., Elmberg, J., Sjöberg, K., Pöysä, H. & Nummi, P. 2006: Experimental evidence for density-dependent survival in mallard (*Anas platyrhynchos*) ducklings. — *Oecologia* 149: 203–213.

Hickey, J. 1952: Survival studies of banded birds. — *U.S. Dep. Int. Fish Wildl. Ser., Special Scientific Report. Wildlife* 15: 1–177.

Hilborn, R. & Mangel, M. 1997: *The ecological detective. Confronting models with data*. — Princeton University Press, New Jersey.

Hill, D., Wright, R. & Street, M. 1987: Survival of mallard ducklings *Anas platyrhynchos* and competition with fish for invertebrates on a flooded gravel quarry in England. — *Ibis* 129: 159–167.

Höhn, E. O. 1948: Mortality of adult and young mallards. — *British Birds* 41: 233–235.

Johnson, D. H., Nichols, J. D. & Schwartz, M. D. 1992. Population dynamics of breeding waterfowl. — In: Batt, B. D. J., Afton, A. D., Anderson, M. G., Ankney, C. D., Johnson, D. H., Kadlec, J. A. & Krapu, G. L. (eds.), *Ecology and management of breeding waterfowl*: 446–485. University of Minnesota Press, Minneapolis.

Johnson, F. A. & Moore, C. T. 1996. Harvesting multiple stocks of ducks. — *J. Wildl. Manage.* 60: 551–559.

Koskimies, J. 1956: Heinäsorsakantamme verotus meillä ja muualla. — *Suomen Riista* 10: 18–25.

Koskimies, P. & Väisänen, R. 1991: *Monitoring bird populations*. — Zoological Museum, Finnish Museum of Natural History, Helsinki.

Lake, B. C., Walker, J. & Lindberg, M. S. 2006: Survival of ducks banded in the boreal forest of Alaska. — *J. Wildl. Manage.* 70: 443–449.

Lebreton, J.-D., Burnham, K. P., Clobert, J. & Anderson, D. R. 1992: Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. — *Ecol. Monogr.* 62: 67–118.

Linkola, P. 1962. Havaintoja sorsalintujen lisääntymistulok-

sesta Keski-Hämeessä [Notes on the breeding success of ducks in Central Häme]. — *Suomen Riista* 15: 157–174. [In Finnish with English summary].

Nichols, J. D., Johnson, F. A. & Williams, B. K. 1995: Managing North American waterfowl in the face of uncertainty. — *Ann. Rev. Ecol. Sys.* 26: 177–199.

Nichols, J. D., Obrecht, H. H. & Hines, J. E. 1987: Survival and band recovery rates of sympatric American black ducks and mallards. — *J. Wildl. Manage.* 51: 700–710.

Nicolai, C. A., Flint, P. L. & Wege, M. L. 2005: Annual survival and site fidelity of northern pintails banded on the Yukon-Kuskokwim delta, Alaska. — *J. Wildl. Manage.* 69: 1202–1210.

Olsen, B., Munster, V. J., Wallensten, A., Waldenström, J., Osterhaus, A. D. M. E. & Fouchier, R. A. M. 2006: Global patterns of influenza A virus in wild birds. — *Science* 312: 384–388.

Olsson, V. 1960: Märkningar och återfynd av svenska gräsänder, *Anas platyrhynchos* L. [Recoveries of marked Swedish Mallards *Anas platyrhynchos* L.]. — *Swedish Wildlife* 2: 87–152. [In Swedish with English summary].

Orthmeyer, D. L. & Ball, I. J. 1990: Survival of mallard broods on Benton Lake National Wildlife Refuge in northcentral Montana. — *J. Wildl. Manage.* 54: 62–66.

Pietz, P. J., Krapu, G. L., Brandt, D. A. & Cox, R. R. Jr. 2003: Factors affecting gadwall brood and duckling survival in prairie pothole landscapes. — *J. Wildl. Manage.* 67: 564–575.

Pirkola, M. K. & Högmander, J. 1974: Sorsapoikueiden iänmääritys [The age determination of duck brood in the field]. — *Suomen Riista* 25: 50–55. [In Finnish with English summary].

Pulliam, H. R. & Danielson, B. J. 1991: Sources, sinks, and habitat selection: a landscape perspective on population dynamics. — *Am. Nat.* 137: 50–66.

Pöysä, H. 1998: Monitoring waterfowl production in Finland. — *Acta Zool. Lit. Ornith.* 8: 52–55.

Pöysä, H. 2001: Dynamics of habitat distribution in breeding mallards: assessing the applicability of current habitat selection models. — *Oikos* 94: 365–373.

Pöysä, H., Elmberg, J., Gunnarsson, G., Nummi, P. & Sjöberg, K. 2004: Ecological basis of sustainable harvesting: is the prevailing paradigm of compensatory mortality still valid? — *Oikos* 104: 612–615.

Pöysä, H., Lammi, E., Väisänen, R. A. & Wikman, M. 1993: Monitoring of waterbirds in the breeding season: the

programme used in Finland in 1986–92. — *IWRB special publication* 26: 7–12.

Reynolds, R. E., Blohm, R. J., Nichols, J. D. & Hines, J. E. 1995: Spring-summer survival rates of yearling versus adult mallard females. — *J. Wildl. Manage.* 59: 691–696.

Rogers, J. P., Nichols, J. D., Martin, F. W., Kimball, C. F. & Pospahala, R. S. 1979: An examination of harvest and survival rates of ducks in relation to hunting. — *Trans. N. Am. Wildl. Nat. Res. Conf.* 44: 114–126.

Rotella, J. J. & Ratti, J. T. 1992: Mallard brood survival and wetland habitat conditions in southwestern Manitoba. — *J. Wildl. Manage.* 56: 499–507.

Sargeant, A. B. & Raveling, D. G. 1992: Mortality during the breeding season. — In: Batt, B. D. J., Afton, A. D., Anderson, M. G., Ankney, C. D., Johnson, D. H., Kadlec, J. A. & Krapu, G. L. (eds.), *Ecology and management of breeding waterfowl*: 396–422. University of Minnesota Press, Minneapolis.

Seber, G. A. F. 1970: Estimating time-specific survival and reporting rates for adult birds from band returns. — *Biometrika* 57: 313–318.

Sheaffer, S. E. 1998: Recruitment models for mallards in eastern North Amercia. — *Auk* 115: 988–997.

Smith, G. W. & Reynolds, R. E. 1992: Hunting and mallard survival, 1979–88. — *J. Wildl. Manage.* 56: 306–316.

Soutiere, E. C. 1989. Survival of hand-reared mallards released in 2 private farms. — *J. Wildl. Manage.* 53: 114–118.

Speek, G., Clark, J. A., Rohde, Z., Wassenaar, R. D. & Van Noordwijk, A. J. 2001: *The EURING exchange-code 2000.* — EURING, the European union for bird ringing, Heteren.

The MathWorks Inc. 2000: *Using MatLab, version 6.* — The MathWorks Inc. 3 Apple Hill Drive, Natick, MA 01760-2098.

Wernham, C. V., Toms, M. P., Marchant, J. H., Clark, J. A., Siriwardena, G. M. & Baillie, S. R. 2002: *The migration atlas: movements of the birds of Britain and Ireland.* — T. & A.D. Poyser, London.

White, G. C. & Burnham, K. P. 1999: Program MARK: survival estimation from populations of marked animals. — *Bird Study (suppl.)* 46: 120–139.

Williams, B. K., Nichols, J. D. & Conroy, M. J. 2002: *Analysis and management of animal populations.* — Academic Press, San Diego.

Appendix. Capture-recapture data for Finnish mallards 1973–2005. *M* is the number of marked birds and *D* is the number of recovered birds.

Year	Adult females		Adult males		Juvenile females		Juvenile males		Unsexed juveniles		Female pulli		Male pulli		Unsexed pulli		Unaged females		Unaged males	
	M	*D*	*M*	*D*	*M*	*D*	*M*	*D*	*M*	*D*	*M*	*D*	*M*	*D*	*M*	*D*	*M*	*D*	*M*	*D*
1973	0	0	0	0	5	0	2	0	37	3	0	0	0	0	34	7	14	1	9	0
1974	0	0	1	0	0	0	0	1	3	0	5	1	11	4	25	2	10	0	5	0
1975	0	0	1	0	10	1	5	0	4	0	11	2	18	5	54	4	14	2	6	0
1976	0	0	0	0	0	0	0	0	1	0	0	0	1	2	118	11	4	2	0	2
1977	0	0	0	0	9	2	12	0	0	0	10	2	8	3	67	6	51	1	33	1
1978	0	0	0	0	6	1	5	0	6	0	2	0	1	0	24	1	54	3	152	8
1979	1	0	2	0	1	1	2	1	0	0	1	2	3	1	19	1	12	3	5	7
1980	0	0	0	0	2	0	2	1	0	1	4	2	4	1	126	12	38	1	49	1
1981	10	1	0	0	16	0	22	4	0	0	15	1	28	1	45	3	43	1	45	2
1982	2	0	0	0	0	1	0	1	2	0	0	0	1	4	96	1	11	5	4	5
1983	0	2	0	1	2	1	3	0	0	0	2	0	1	2	51	3	2	1	1	2
1984	1	0	0	0	2	0	1	0	2	0	0	0	2	0	59	1	9	0	0	1
1985	1	0	0	0	0	1	0	2	0	0	4	3	5	2	107	3	10	4	7	2
1986	2	0	0	0	1	0	4	1	1	0	0	0	0	0	19	2	9	1	2	2
1987	0	0	1	0	0	0	2	0	0	0	2	2	3	2	29	3	6	0	0	1
1988	7	0	0	0	2	0	0	0	0	0	5	3	4	2	29	1	7	0	2	1
1989	0	0	0	0	1	0	0	0	0	0	3	0	5	3	185	8	4	1	0	0
1990	6	0	0	0	0	0	0	0	2	0	0	1	2	2	44	6	13	2	2	0
1991	5	0	3	1	1	0	0	0	2	0	1	0	2	1	57	1	10	2	13	1
1992	12	0	2	0	3	0	5	0	0	0	3	1	11	2	44	4	8	0	6	3
1993	16	1	3	0	2	0	0	0	1	0	3	1	16	4	15	3	12	1	2	0
1994	10	0	5	1	1	0	3	1	0	0	11	3	5	4	20	1	8	0	2	0
1995	8	2	5	1	8	0	7	0	0	0	8	0	6	2	21	1	7	0	3	2
1996	8	2	2	0	3	0	0	1	3	0	0	0	0	1	13	2	10	0	3	0
1997	7	0	1	0	2	1	4	0	1	0	0	1	3	1	11	1	11	2	3	2
1998	8	1	0	0	3	0	0	0	2	0	3	0	3	0	2	0	9	1	0	0
1999	5	0	0	0	3	0	2	0	0	0	0	0	0	0	16	0	12	0	1	1
2000	31	1	27	0	3	0	6	0	2	0	3	0	0	0	21	0	10	0	0	0
2001	1	2	0	0	5	0	4	0	0	0	2	0	4	2	6	0	13	3	4	0
2002	1	0	0	0	1	2	1	1	0	0	0	0	1	0	5	1	8	1	1	0
2003	2	0	1	0	10	0	9	1	0	1	13	0	5	0	1	0	30	0	6	1
2004	1	0	0	0	10	0	7	0	0	0	17	2	19	1	13	0	11	0	3	0
2005	1	0	0	0	21	2	25	3	0	0	12	4	16	4	5	0	11	0	5	2
Total	**146**	**12**	**54**	**4**	**133**	**13**	**133**	**18**	**69**	**5**	**140**	**31**	**188**	**56**	**1381**	**89**	**481**	**38**	**374**	**47**