

Article

Population Trend of Colonially Nesting Heron Species in Greece

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Simple Summary: We studied the nesting population trends of the colonially nesting heron species in Greece from 1988 to 2018, aiming to identify drivers of these trends and thus inform colony/wetland conservation measures. Two species (Cattle Egret and Squacco Heron) had a positive trend, while three species (Black-crowned Night Heron, Little Egret and Grey Heron) had a negative trend. The Purple Heron presented a stable trend. Our results suggest that: (a) The Natura 2000 network and the operation of the protected areas Management Authorities have positively affected heron species nesting population trend or range expansion, (b) national wetland restoration efforts have facilitated the expansion of most heron species' breeding range via the establishment of new colonies, and (c) colonies located outside protected areas were—especially in the case of the Grey Heron—most likely to have a declining nesting population trend. The drivers behind the observed population trends differed among species, even among those sharing the same breeding sites. This suggests that the nesting population trends could be due to ecological changes at both the breeding and at the wintering sites. Our results emphasize the importance of continuing wetland restoration efforts, developing heron-friendly farming practices, and adopting a systematic nationwide survey of colonies.

Abstract: Heron colonies are dynamic components of wetlands. Therefore, their systematic monitoring is important for the management of both birds and wetlands. During the period 1988–2018, we counted breeding pairs of seven colonial breeding heron species at 65 colonies across 37 wetlands in Greece. We considered as annual variables of a population: (a) years since 1988, (b) Natura 2000 network inclusion, (c) protected area management authority overseeing, (d) wetland type (new or restored), and (e) new colonies (established after 2003). The Cattle Egret *Bubulcus ibis* and the Squacco Heron *Ardeola ralloides* had a positive breeding population trend. The Black-crowned Night Heron *Nycticorax nycticorax*, Little Egret *Egretta garzetta*, and Grey Heron *Ardea cinerea* had a negative trend, while the Purple Heron *Ardea purpurea* population was stable. The Great White Egret *Ardea alba* bred sporadically at only a few sites which precluded the evaluation of its population trend. The informative population variables differed among species, even of those at the same colony, which suggests trends are also affected by conditions at wintering grounds. The study highlights the need for the systematic monitoring of heron colonies and the protection of foraging/breeding areas in order to reverse the observed negative population trends.

Keywords: Ardeidae; egrets; heron colonies; TRIM; wetlands; conservation



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1. Introduction

Nesting bird colonies are dynamic as they may change location, size, and nesting species composition over the years. Recording and identifying potential causes of such changes can assist in developing corrective management actions where and when necessary [1,2]. The importance of the long-term monitoring of heron colonies for the successful management of breeding species and their wetland habitats is recognized, which is why many western European countries have adopted such monitoring schemes. In the UK, for instance, monitoring—especially for the Grey Heron—has been carried out since 1928, while in France, Spain, and Italy heron populations are systematically monitored since the 1960s or the 1970s [3–8].

All nine species of the family Ardeidae nesting in Europe breed in Greece [4,5]; Bittern *Botaurus stellaris*, Little Bittern *Ixobrychus minutus*, Little Egret *Egretta garzetta*, the Black-crowned Night Heron *Nycticorax nycticorax*, Squacco Heron *Ardeola ralloides*, Cattle Egret *Bubulcus ibis*, Purple Heron *Ardea purpurea*, Grey Heron *Ardea cinerea*, and Great White Egret *Ardea alba*, of which all but the two bittern species nest colonially. Two species are threatened according to the Red Data Book of the threatened Animals of Greece (Purple Heron—endangered; Great White Egret—vulnerable; [9]). The monitoring of the largest heron colonies commenced in Greece in the 1980s [10,11], while nation-wide heron colony surveys were carried out four times (2003, 2009, 2014, and 2018). Based on the mean number of breeding pairs in the last four surveys and the European population estimates according to IUCN Red Data list (Table A1), Greek wetlands are home to approximately 3% of the Little Egret, 2.4% of Squacco Heron, and 1.8% of Black-crowned Night Heron European populations, indicating the international importance of Greek wetlands for heron conservation [4,11,12].

While there are >1400 wetlands (including river deltas and their estuaries; freshwater lakes—natural or artificial; and coastal marshes) in Greece, covering approximately 2% of the land area, three quarters of them are small, accounting for 1% of the total wetland area [13]. Ten of the larger ones are included in the Ramsar list of wetlands due to their international importance for bird conservation [14]. Almost all larger wetlands have one or more heron colonies. The number of colonies and overall nest number of colonially nesting heron species have more than doubled from 1985 to 2009 (1985: 21 colonies with 2500–3000 nests; 2003: 33 colonies and 5589 nests; 2009: 44 colonies with 6097 nests) [10,11,15]. Increases in the number of colonies and nesting pairs were also concurrently recorded in other colonially nesting wetland birds such as the Spoonbill *Platalea leucorodia* [16], Glossy ibis *Plegadis falcinellus* [15], Great Cormorant *Phalacrocorax carbo* [17], and the Great White *Pelecanus onocrotalus* and Dalmatian *Pelecanus crispus* pelicans [18]. The increase was probably related to better protection following the establishment in 2003 of protected area Management Authorities for national parks, which included most large wetlands containing the vast majority of heron colonies [11,15].

Despite their importance for water birds, wetlands in Greece face many threats. In the 1980s and 1990s water pollution and drainage were among the main threats to wetlands. These threats persist, even though 80% of wetlands are within protected areas (Natura 2000 network, national parks) [13]. However, during the 21st century, some previously drained wetlands have been restored and peoples' attitude towards wetlands started to change as a result of public awareness campaigns. At the same time, new threats emerged for the heron colonies, primarily due to changes in human activities around wetlands such as agricultural intensification (e.g., rice cultivation) and disturbance (e.g., recreational activities).

The aim of the present study was to examine the available data on colonially nesting heron species in Greece for 31 years (1988–2018) in order to estimate the population trend of individual species, which may differ from the increasing trend observed in the overall number of colonies and nests. Moreover, we discuss possible drivers of the observed trends, which is a necessary first step for designing and implementing targeted conservation measures where and when needed.

2. Materials and Methods

2.1. Study Areas

The study includes data from all wetlands and wetland complexes with known heron colonies in mainland Greece and the islands (Figure 1, Table 1). Fifty-one (79%) of these colonies were within Natura 2000 sites and six (9%) were in new/restored wetlands. Six colonies were situated in suburban parks (e.g., Kerkyra) or trees at the edge of a town (e.g., Kastoria, Aridaia), and therefore can be considered urban colonies (Table 1). There were seven known heron colonies were not included in the analysis due to lack of data (Taka Lake, Hotousa, Oxia island, Prasso islet, and three colonies at the Prespa Lakes, located in northwestern Greece at the tri-state conjunction with Albania and Northern Macedonia).



Figure 1. Distribution of wetlands with heron colonies in Greece in 2018 (large dots = colonies with >501 nests; medium dots = colonies with 101–500 nests; small dots = colonies with <100 nests). Numbers refer to Table 1 wetland names.

Table 1. List of wetlands with heron colonies included in this study, along with information on nesting species (AC: *Ardea cinerea*; EG: *Egretta garzetta*; NN: *N. nycticorax*; AR: *Ardeola ralloides*; BI: *Bubulcus ibis*; AP: *Ardea purpurea*; AA: *Ardea alba*), protection status, and type of wetland (U: urban; N: new wetland).

a/a	Wetland Name	a/a	Colony Name	Species Nesting	Protected Area
1	Evros River	1	Dikaia	AC, EG, NN	Yes
		2	N. Vissa	AC, EG, NN	Yes
2	Evros Delta	3	Evros Delta	AP	Yes
3	Ismarida Lake	4	Ismarida Lake	AP	Yes
4	Porto Lagos Lagoon	5	Porto Lagos	AC, EG, AR, BI	Yes
5	Nestos River estuary	6	Keramoti	AC, EG, NN	Yes
		7	Thassopoula (Island)	EG	Yes
6	Kerkini Lake (artificial)	8	Kerkini	AC, EG, NN, AR, AP, BI, AA	Yes
		9	Limnochori	AC, NN	Yes
7	Strymon River	10	Kouvouklio	AC	No
		11	Strymon River	EG, AA	No
8	Volvi–Koronia Lakes (partially, Koronia Lake, restored)	12	Big plane tree	AC	Yes
		13	Small plane tree	AC	Yes
		14	Apollonia forest main	AC	Yes
		15	Apollonia forest east	EG	Yes
		16	Koronia west	EG, NN, AR, AP, AA	Yes
		17	Koronia east	AC	Yes
9	Axios–Aliakmon–Gallikos Deltas (partially, N. Agathoupolis Marsh, restored, N)	18	Axios Delta main	AC, EG, NN, AR, BI, AA	Yes
		19	Axios danio	AP	Yes
		20	Gallikos River old	EG, AR	Yes
		21	Gallikos Riner new	AC	Yes
		22	N. Agathoupolis	AP	Yes
10	Sani marsh (restored, N)	23	Sani	AC, EG, NN, AP	Yes
11	Aliakmon River	24	Kouloura	AC, EG	No
12	Almopaios River	25	Aridaia (U)	AC	Yes
		26	Krania Almopias	AC	Yes
13	Petron Lake	27	Petron	AC, EG, NN, AR, AP	Yes
14	Chimaditida Lake	28	Chimaditida	AP	Yes
15	Kastoria Lake	29	Kastoria Lake (U)	AC, EG, NN	Yes
		30	Kastoria town (U)	NN	Yes
16	Grevenitis River	31	Grevenitis	AC	No
		32	Rimnio	AC	No
17	Polifitou Lake (partially artificial)	33	Velvendos	AC, EG	No
		34	Velvendos cormo	AC	No
		35	Ilarion Dam	EG	No
18	Elassona River	36	Elassona	AC	Yes
19	Tyrnavos Lake-pond (artificial)	37	Mati Tyrnavos	AC	No

Table 1. Cont.

a/a	Wetland Name	a/a	Colony Name	Species Nesting	Protected Area
20	Neochoritis River	38	Neochoritis	AC, EG	Yes
21	Trikala Marsh (artificial, N)	39	Trikala	EG, NN, AR	No
		40	Glafki	AC, EG, NN, AR	Yes
		41	Galini (U)	AC	Yes
		42	Platycampos (U)	AC	Yes
22	Karla Lake (restored, N)	43	Karla Lake	EG, NN, AR, AP, AA	Yes
		44	Kanalia	AC, NN	Yes
23		Spercheios Delta	45	Spercheios	EG, NN
24	Pamvotia Lake	46	Ioannina	AC	Yes
		47	Sagiada	AC, EG, NN, AR	Yes
		48	Thesprotia	AC, AR	Yes
25	Kalamas River estuary	49	Prassoudi islet (Island)	EG, AR, BI	Yes
		50	Kerkyra (Corfu), (U)	AC	No
26	Kerkyra Marsh (Corfu Island)	51	Caparelli	EG	No
27		Acheron River estuary	52	Acheron	AC, EG, NN, AR, AP
28	Kalodiki Lake	53	Kalodiki	AC, EG, NN, AR	Yes
		54	Rodia marsh	EG, NN, AR, AP	Yes
		55	Psathotopi	AP	Yes
29	Amvrakikos wetland	56	Korakonisia (Island)	EG, BI	Yes
		57	Gaidouronisi (Island)	EG	Yes
30	Amvrakia Lake	58	Amvrakia	EG, NN, AR, AP, BI	Yes
31	Limnopoula Lake	59	Limnopoula	AC	Yes
32	Smokovo River	60	Smokovo	AC	No
33	Messolonghi–Acheloo Delta	61	Messolonghi	EG, NN, AR, AP	Yes
34	Prokopos Marsh	62	Prokopos	AP	Yes
35	Stymfalia Lake	63	Stymfalia	AP	Yes
36	Evrotas River estuary	64	Evrotas	AC, EG, AR	Yes
37	Gadouras Dam Lake (N)	65	Rhodos (Island)	EG	No

Management actions within the Natura 2000 sites commenced only after the establishment of the first protected area Management Authorities in 2003. Ten of those Management Authorities had existing heron colonies within their jurisdictions. In effect, heron colony conservation commenced from that point on.

Using mostly European Union funds, several efforts to restore degraded or drained wetland have taken place [19]. The first and largest restored wetland was Karla Lake (c. 3800 ha) in Thessaly, central Greece, in 2000, followed by many smaller wetlands [19–22] (Table 1; Figure 1). In addition, at least 54 reservoirs were built in Greece from 2003 to 2012 [23], either for irrigation purposes or to restore previously drained wetlands. In some of these new or restored wetlands, heron and/or Great Cormorant colonies were established (e.g., at the restored Sani and N. Agathoupolis marshes and Koronia Lake in northern Greece, and the new pond built in Trikala, central Greece; Table 1).

The species considered in this study are all the colonially nesting heron species breeding in Greece; Little Egret, Black-crowned Night Heron, Squacco Heron, Cattle Egret, Purple Heron, Grey Heron, and Great White Egret. Five species were not included either because

they are not colonial breeders (Bittern and Little Bittern) or because they are only sporadically reported and not known to breed in Greece (Western Reef Heron *Egretta gularis* in 2008 [24]; Black Heron *Egretta ardesiaca* in 2012 [25], Green-backed Heron *Butorides striatus* in 2019—see F. Samaritakis, pers. comm.). We did not include other species often breeding within heron colonies in this study, such as the Spoonbill *Platalea leucorodia*, Glossy Ibis *Plegadis falcinellus*, Pygmy Cormorant *Microcarbo pygmaeus*, Great Cormorant *Phalacrocorax carbo*, and Crested Grebes *Podiceps cristatus*.

The data used for this study are from (a) four national surveys of heron colonies, nesting species and their populations (number of nests) conducted in 2003, 2009, 2014, and 2018; (b) surveys at most (but not all) colonies in 1988, 1989, 1990, and 2015; and (c) more frequent surveys (often yearly) performed at six wetlands (Porto Lagos, Nestos Delta, Kerkini Lake, Axios Delta, Koronia—Volvi Lakes, and Kalamas Delta; Table 1).

2.2. Inventory of Colonies

All possible areas that can host a heron colony were visited during the four national colony surveys, utilizing information collected from local birdwatchers [26]. During the field visit, the coordinates, nest tree species and predominant tree species, number of breeding pairs per species, and possible anthropogenic threats were recorded for each colony.

2.3. Nest Count

The number of each species' nests was recorded during the peak of the chick rearing period (late May–early June, [11]). At four colonies (at Axios Delta and the Kerkini and Koronia Lakes), a second visit was carried out (until mid-June) specifically for counting Squacco Heron nests, as the species starts nesting later compared to other heron species. Nests were counted from a distance either from the ground or from boat, outside the colony, using binoculars and/or telescopes. In the case of three colonies (one colony at Amvrakikos and two colonies at the Volvi and Koronia Lakes), which were either inaccessible on foot or by boat or the nests were located within thick foliage or reedbed and not visible, we estimated the number of nests by tallying the departing birds of each species for the feeding grounds for one hour after dawn, assuming that two birds corresponded to one nest [27]. The nests of Grey Heron colonies were counted in April, as this species starts breeding as early as February. Given the nesting trees typically used by this species, a May–June count of nests would have been problematic due to thick foliage. For this reason, in some colonies, we counted the nests by entering the colony in the morning (6–9 a.m.) either on foot (Axios Delta) or by boat (Kerkini, Kastoria Lakes) and using binoculars.

2.4. Trend Analysis

To estimate the nest population trend of a species across the study period while taking into consideration the years with no survey data, we used the Trends and Indices for Monitoring Data (TRIM) software vers. 2.1.1 [28], which was developed specifically for analyzing data from incomplete wildlife surveys using log linear Poisson regression models [29]. TRIM is widely used in estimating breeding bird population trends [7]. In addition to the mandatory “Time” variable, which refers to the years elapsed since the first survey year (1988), we considered four additional colony parameters which could explain the observed changes in a species' nests in monitored colonies:

- (a) “Natura 2000”, which indicates if the colony was situated within the Natura 2000 network of protected areas.
- (b) “Management Authority”, which indicates if the colony was situated within the jurisdiction of a protected area management authority (as of 2003, the year these authorities were established in Greece).
- (c) “New/restored wetland”, which indicates if the colony was in a wetland that was either established (new) or restored after 2003.
- (d) “New colony”, which indicates if the heron colony was a colony established after 2003.

Data from all 1988–2018 surveys were combined. Colonies with three or less counts were excluded from the analysis. Missing counts (i.e., imputed values) ranged from 12% for the Cattle Egret to 53% for the Grey Heron. The Akaike Information Criterion (AIC) was used for model selection [30]. In order to have an optimal set of informative variables while managing for model complexity, we first ran univariate models of each parameter against the baseline model (i.e., model that includes as covariates only time—i.e., elapsed years since 1988—and site). Only informative variables (i.e., with univariate models having <AIC than the baseline model) were included in multivariate combinations. Population trends (i.e., slopes) were computed along with associated confidence intervals (CI) at the 5% significance level and interpreted using the following classification [28].

- (a) Strong increase: more than 5%/year (lower CI limit > 0.05).
- (b) Moderate increase: less than 5%/year (lower CI limit > 0.0).
- (c) Stable: no significant increase or decline ($-0.05 < \text{lower} < 0.0 < \text{upper} < 0.05$).
- (d) Moderate decrease: less than -5% /year (upper CI limit < 0.0).
- (e) Strong decrease: more than -5% /year (upper CI limit < 0.05).
- (f) Uncertain, any other case.

3. Results

In total, 65 heron colonies in 37 wetlands were surveyed at least once during the study period (Figure 1; Table 1). Of the four national surveys (2003, 2009, 2014, 2018), the highest number of active colonies was in 2009 ($n = 44$), when the highest number of heron nests (all species) was also recorded (6097). In 2014, the total nests were 5903 in 43 colonies, while 5589 nests in 33 colonies and 4853 nests in 32 colonies were recorded in 2003 and 2018, respectively.

Hérons often formed mixed colonies. However, Grey and Purple Herons, Little Egrets, and, rarely, Black-crowned Night Herons formed mono-specific colonies as well. Of the 34 (52%) monospecific colonies, most ($n = 19$) were Grey Heron colonies. The rest were colonies of Purple Herons ($n = 8$), Little Egrets ($n = 6$), and Black-crowned Night Herons ($n = 1$) (Table 1).

The nest population trend of the study species differed (Table 2). The Cattle Egret and the Squacco Heron were the species with an increasing trend (strong and moderate, respectively), while three species showed a decreasing trend (Black-crowned Night Heron—strong decrease, Grey Heron and Little Egret—moderate decrease). The Purple Heron population appeared to be stable. The Great White Egret nested sporadically, with small number of nests and at a few sites only, so its population trend could not be evaluated (Table 2).

Table 2. Herons' nesting population trend (regression model taking into consideration the coefficient "Time") and their colonies' characteristics in Greece during the study period, 1988–2018.

Species	Nesting Population Trend—Slope β (se) and p -Value	Mean Number of Nests/Colony \pm SD (Min.–Max.)	Number of Colonies (Wetlands)	Colonies in Protected Areas
Little Egret	Moderate decrease -0.014 (0.001) $p < 0.001$	226.6 ± 125.2 (1–902)	33 (25)	27
Black-crowned Night Heron	Strong decrease -0.099 (0.008) $p < 0.001$	285.8 ± 297.4 (2–980)	22 (17)	21
Squacco Heron	Moderate increase 0.01 (0.014) $p < 0.001$	78.4 ± 118.4 (1–501)	17 (17)	16
Cattle Egret	Strong increase 0.159 (0.016) $p < 0.001$	26.1 ± 38.5 (1–113)	6 (6)	6

Table 2. Cont.

Species	Nesting Population Trend—Slope β (se) and p -Value	Mean Number of Nests/Colony \pm SD (Min.–Max.)	Number of Colonies (Wetlands)	Colonies in Protected Areas
Purple Heron	Stable −0.003 (0.005) $p = 0.49$	8.0 \pm 5.5 (1–25)	17 (14)	14
Grey Heron	Moderate decrease 0.058 (0.005) $p < 0.01$	95.9 \pm 87.0 (1–320)	39 (26)	30
Great White Egret	Not evaluated	4.7 \pm 10.4(1–39)	5 (5)	4

The species with the largest average number of nests per colony were the Black-crowned Night Heron (285.8 \pm 297.4) and the Little Egret (226.6 \pm 125.2). Conversely, the Purple Heron had on average the lowest number of nests per colony (8.0 \pm 5.5; Table 2).

3.1. Little Egret (*Egretta garzetta*)

In 2018, the Little Egret was the most numerous heron species in terms of total nests (2083) and the second most widespread in terms of number of colonies ($n = 16$). Most (91.2%) of the nests were located in six colonies in northern and western Greece (Kerkini Lake, Axios Delta, Porto Lagos, Keramoti, Prassoudi, and Rodia in the Amvrakikos wetland, Figure 1; Table 1). The highest number of nests was recorded in 2009 ($n = 2506$) with breeding taking place in 19 colonies. The moderate population decrease observed (Figure 2; Table 2) was characterized by a concurrent decrease in the mean number of nests per colony and an increase in the number of colonies (Figure 3). Fourteen new colonies were established after 2003, of which most ($n = 9$) were within protected areas (six in areas actively protected by the respective Management Authority). At least four of these new colonies (including three of those actively protected) were later abandoned.

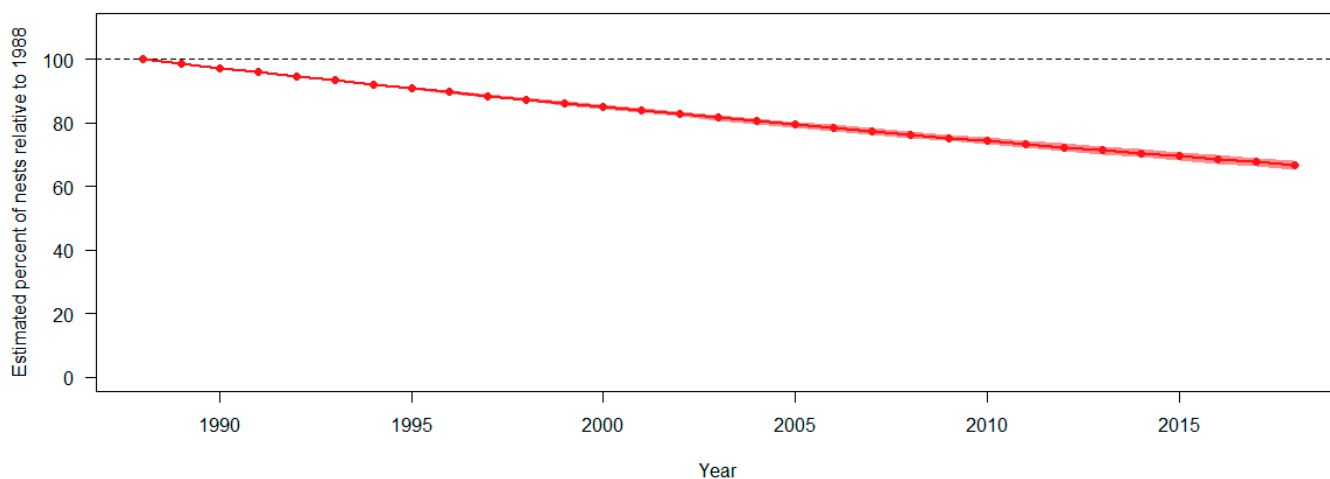


Figure 2. Nest population trend of the Little Egret *Egretta garzetta* in the 1988–2018 period in Greece (moderate decrease). The red dots indicate the percentage of nests in a given year relative to the 1988 nest population, as estimated from the fitted model values of the best model (% of imputed values: 48). Dashed line marks the estimated percent of nests in 1988.

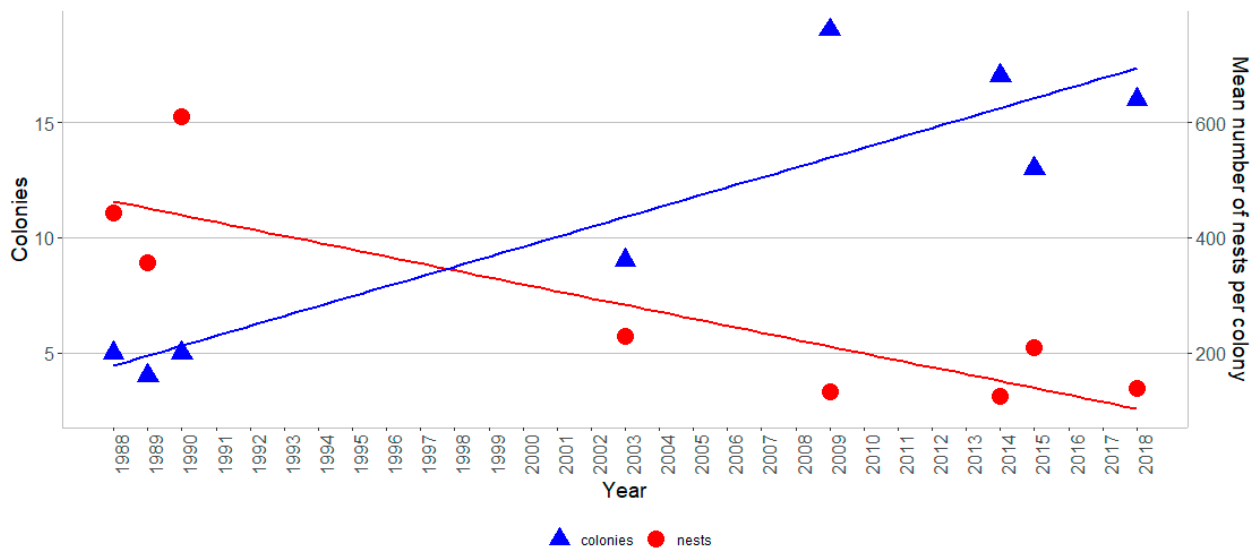


Figure 3. Changes in the number of Little Egret *Egretta garzetta* colonies ($F = 25.54$, $df = 6$, $R^2_{adj} = 0.778$, $p = 0.002$) and the mean number of nests per colony ($F = 17.64$, $df = 6$, $R^2_{adj} = 0.704$, $p = 0.006$) in the 1988–2018 period in Greece.

3.2. Black-Crowned Night Heron (*Nycticorax nycticorax*)

In 2018, the Black-crowned Night Heron was the species with the highest average number of nests per colony and the third most widespread in Greece (Table 2). The highest number of nests was recorded in 2009 ($n = 1484$ nests) with breeding taking place in 15 colonies. There were thirteen active colonies in 2018, and 87.4% of the nests were located in three colonies in northern and western Greece (Kerkini Lake, Axios Delta, Amvrakikos, Figure 1; Table 1). The strong population decrease observed (Figure 4; Table 2) was characterized by a concurrent decrease in the mean number of nests per colony and an increase in the number of colonies where the species occurs (Figure 5). Twelve new colonies were established after 2003, of which most (11) were within protected areas (eight in areas actively protected by the respective Management Authority). At least five of these new colonies (including four of those actively protected) were later abandoned. Colonies that were established in new/restored wetlands and located within areas where a protected management authority was operating had a significantly lower decreasing trend (Table 3).

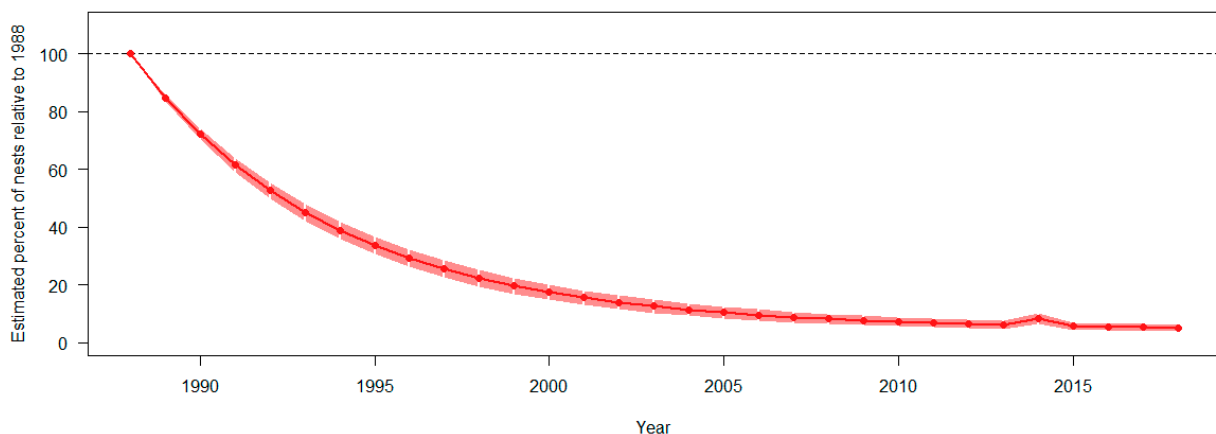


Figure 4. Nest population trend of the Black-crowned Night Heron *Nycticorax nycticorax* during the 1988–2018 period in Greece (strong decrease). The red dots indicate the percentage of nests in a given year relative to the 1988 nest population, as estimated from the fitted model values of the best model (% of imputed values: 40). Dashed line marks the estimated percent of nests in 1988.

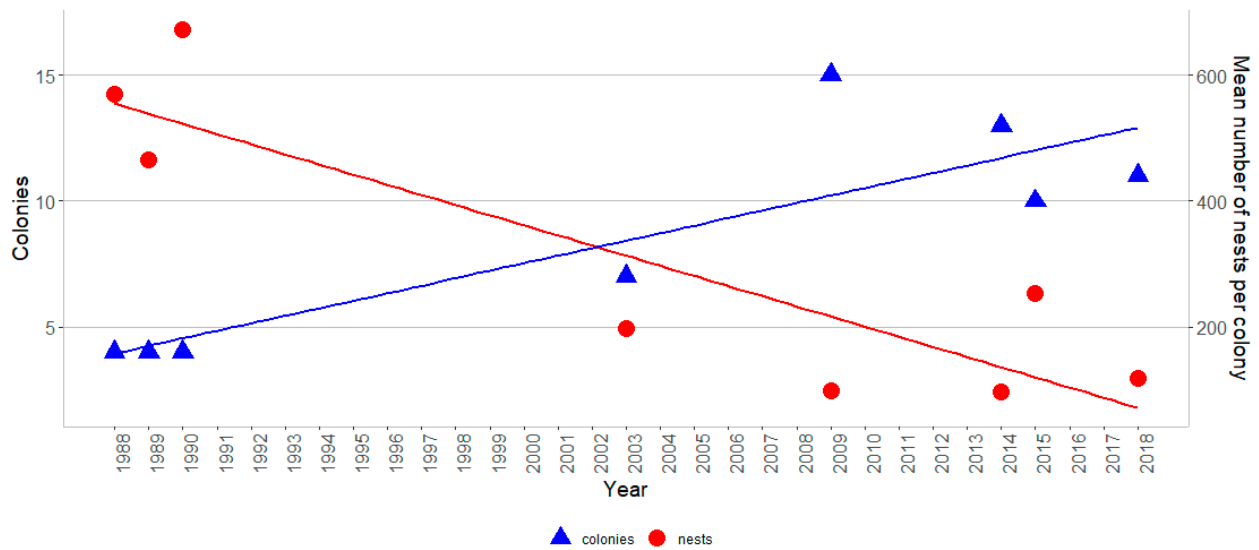


Figure 5. Changes in the number of Black-crowned Night Heron *Nycticorax nycticorax* colonies ($F = 17.24$, $df = 6$, $R^2_{adj} = 0.699$, $p = 0.006$) and the mean number of nests per colony ($F = 22.5$, $df = 6$, $R^2_{adj} = 0.754$, $p = 0.003$) during the 1988–2018 period in Greece.

Table 3. Beta coefficients of the best regression model of the nesting heron population trend in Greece, 1988–2018 [β (se)].

Species/Coefficient	Intercept *	Within a Natura 2000 Site	Under a Management Authority (after 2003)	New or Restored Wetland (since 2003)	New Colony (Established after 2003)
Little Egret	−0.013 (0.001)	-	-	-	-
Black-crowned Night Heron	−0.18 (0.011)	n/a **	0.153 (0.011)	0.173 (0.009)	-
Squacco Heron	0.009 (0.001)	-	-	0.158 (0.016)	0.054 (0.008)
Cattle Egret	0.159 (0.016)	n/a **	-	n/a **	-
Purple Heron	0.137 (0.067)	n/a **	−0.15 (0.067)	-	0.277 (0.037)
Grey Heron	−0.16 (0.009)	0.089 (0.012)	0.063 (0.009)	-	0.162 (0.009)

* The intercept contains the SITE and YEAR (elapsed since 1988). ** There was no variation of that variable among the species’ colonies and therefore the variable was not included in multivariate models’ selection.

3.3. Squacco Heron (*Ardeola ralloides*)

In 2018, the Squacco Heron was the fourth most widespread heron species during the study period (Table 2). The highest number of nests was recorded in 2015 ($n = 804$ nests) with breeding taking place in seven colonies. There were nine active colonies in 2018, and 91.5% of the nests were in two colonies in northern and western Greece (Kerkini Lake and Axios Delta Figure 1; Table 1). The moderate population increase observed (Figure 6; Table 2) was characterized by a concurrent significant increase in the number of active colonies and a decrease (not statistically significant) in the mean number of nests per colony (Figure 7). Nine new colonies were established after 2003, of which most (eight) were within protected areas (seven in areas actively protected by the respective Management Authority). At least seven of these colonies (all within protected areas), were later abandoned. Colonies located in new/restored wetlands and/or established after 2003 appear to have a more positive population trend (Table 3).

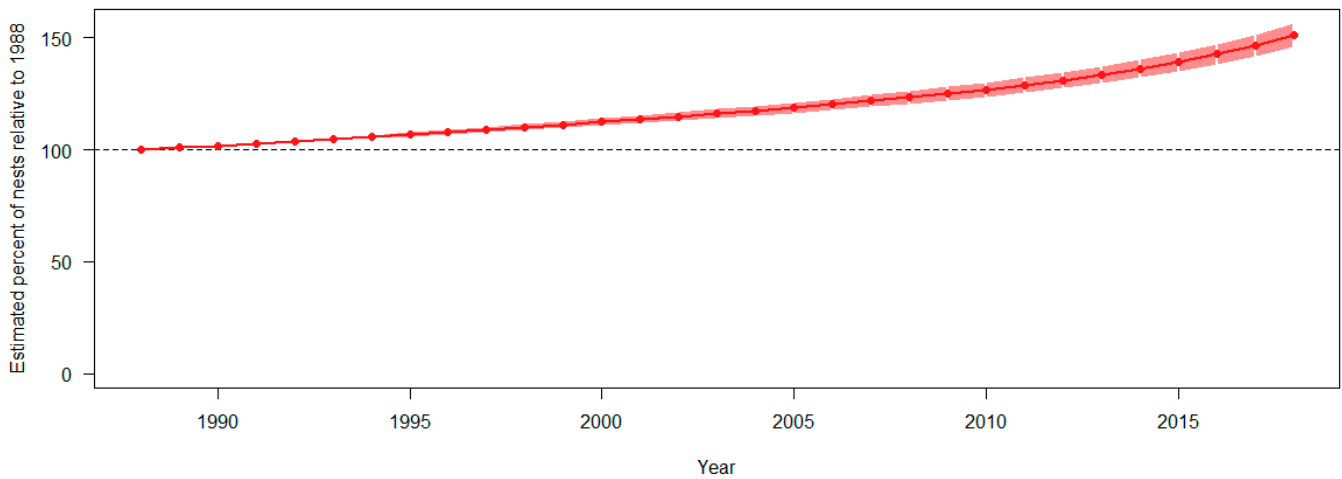


Figure 6. Nest population trend of the Squacco Heron *Ardeola ralloides* during the 1988–2018 period in Greece (moderate increase). The red dots indicate the percentage of nests in a given year relative to the 1988 nest population, as estimated from the fitted model values of the best model (% of imputed values: 43). Dashed line marks the estimated percent of nests in 1988.

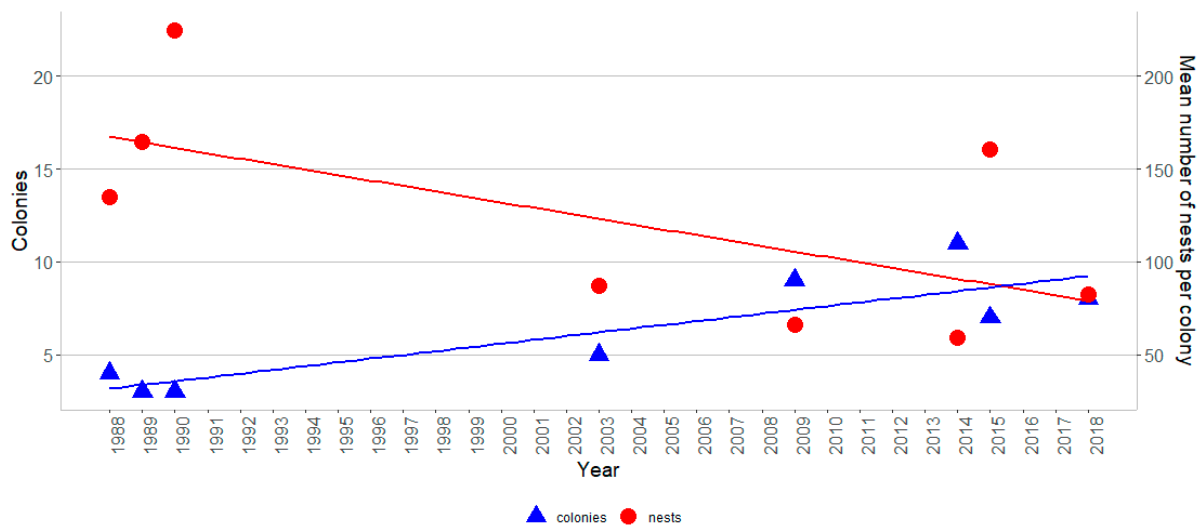


Figure 7. Changes in the number of Squacco Heron *Ardeola ralloides* colonies ($F = 17.19$, $df = 6$, $R^2_{adj} = 0.698$, $p = 0.006$) and the mean number of nests per colony ($F = 4.05$, $df = 6$, $R^2_{adj} = 0.304$, $p = 0.091$) during the 1988–2018 period in Greece.

3.4. Cattle Egret (*Bubulcus ibis*)

The Cattle Egret is the most recently established heron species in Greece, with the first breeding nests recorded in 1991. Since then, the species gradually expanded its distribution and increased its population (Figure 8). It started to systematically breed in the country as of 2009. The highest numbers were recorded in 2016 ($n = 125$ nests) with breeding taking place in seven colonies, always mixed with nests of other heron species, in six protected wetlands, namely Kerkini Lake, Axios Delta, Porto Lagos Lagoon, Amvrakikos, Amvrakia Lake, and Kalamas Delta (Figure 1; Table 1). The largest colony (Prassoudi islet)—located on a rocky islet in the Ionian Sea—contained 89.6% of the nesting population in Greece in 2016. The nesting sites gradually expanded from western to north-eastern Greece and the mean number of nests per colony also increased (Figure 9). Five new colonies were established after 2013, of which most (four) were within protected areas and actively protected by the respective Management Authority. All the new colonies remained active until 2018. Since the establishment of regular breeding colonies in 2009, the species has seen a strong

population increase, without any colony parameter being a significant predictor of this trend (Table 3).

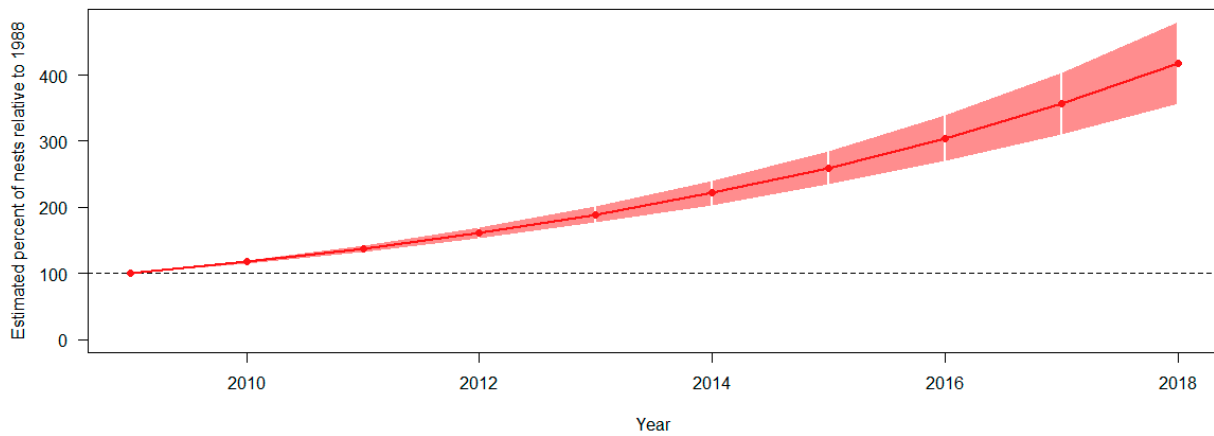


Figure 8. Nest population trend of the Cattle Egret *Bubulcus ibis* during the period 1988–2018 in Greece (strong increase). The red dots indicate the percentage of nests in a given year relative to the 1988 nest population, as estimated from the fitted model values of the best model (% of imputed values: 12). Dashed line marks the estimated percent of nests in 1988.

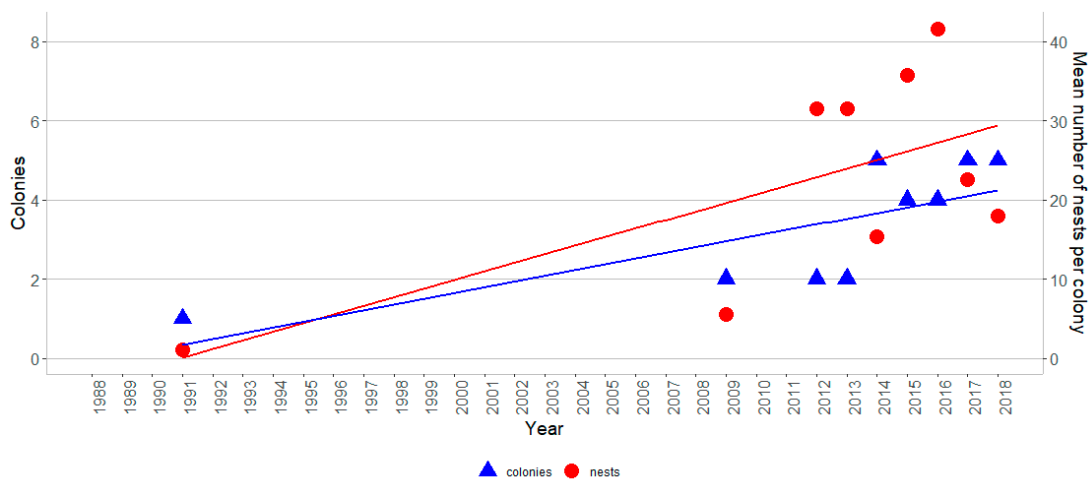


Figure 9. Changes in the number of Cattle Egret *Bubulcus ibis* colonies ($F = 9.03$, $df = 6$, $R^2_{adj} = 0.501$, $p = 0.019$) and the mean number of nests per colony ($F = 5.04$, $df = 6$, $R^2_{adj} = 0.335$, $p = 0.059$) during the period 1988–2018 in Greece.

3.5. Purple Heron (*Ardea purpurea*)

The Purple Heron was recorded nesting only in wetlands located within the Natura 2000 network (Table 1). The highest number of nests was recorded in 2014 ($n = 56$ nests) with breeding taking place in 12 colonies. The population was roughly equally spread across small colonies. The population trend was stable (Table 3; Figure 10) but was characterized by a concurrent significant decrease in the mean number of nests per colony and a significant increase in the number of colonies where the species occurs (Figure 11). Eleven new colonies were established after 2003, all of which were within protected areas (seven in areas actively protected by the respective Management Authority). At least three of these colonies (two actively protected) were later abandoned. Colonies established after 2003 appear to be doing better, unlike those located within areas where a Management Authority was operating (Table 3).

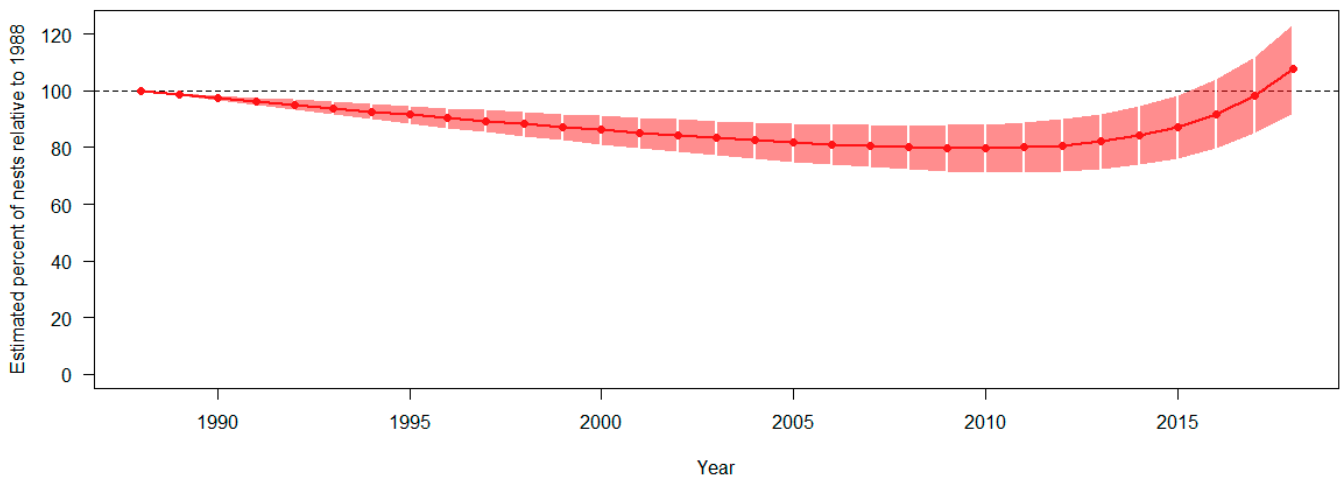


Figure 10. Nest population trend of the Purple Heron *Ardea purpurea* during the period 1988–2018 in Greece (stable). The red dots indicate the percentage of nests in a given year relative to the 1988 nest population, as estimated from the fitted model values of the best model (% of imputed values: 25). Dashed line marks the estimated percent of nests in 1988.

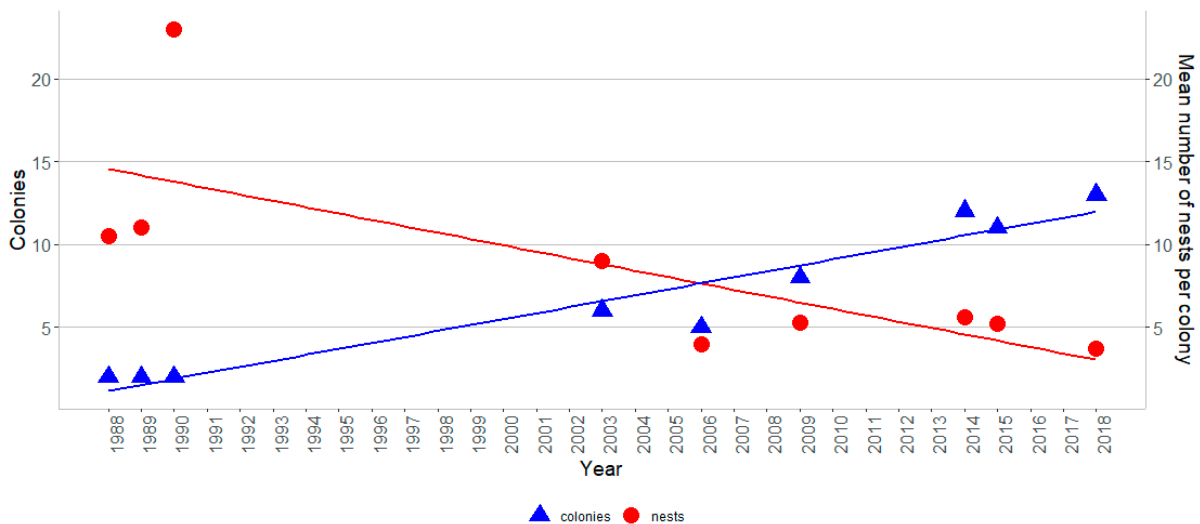


Figure 11. Changes in the number of Purple Heron *Ardea purpurea* colonies ($F = 84.64$, $df = 6$, $R^2_{adj} = 0.913$, $p < 0.001$) and the mean number of nests per colony ($F = 8.97$, $df = 6$, $R^2_{adj} = 0.99$, $p = 0.02$) during the period 1988–2018 in Greece.

3.6. Grey Heron (*Ardea cinerea*)

In 2018, the Grey Heron was the most widespread heron species and the second most numerous in Greece after the Little Egret (Table 2). The highest number of nests was recorded in 2014 ($n = 1539$ nests) with breeding taking place in 23 colonies. The active colonies in 2018 were 24, and 65% of the nests (644) were located in four colonies in northern (Kerkini Lake, Limnochori, Porto Lagos, and Keramoti, Figure 1; Table 1). The species maintained a significant proportion of its breeding population outside protected areas in 2009 (eleven colonies; a 28.9% of total nests), but only five of these colonies remained in 2018—the rest either shifted to sites within protected areas or collapsed. The moderate population decrease observed during the study period (Figure 12; Table 2) is characterized by a concurrent significant decrease in the mean number of nests per colony and a significant increase in the number of heron colonies during the 1988–2003 period (Figure 13). Both of these metrics stabilized after 2003. Seven new colonies were established after 1990, of which most (six) were within protected areas (five in areas actively protected by the respective Management Authority). At least six of these colonies (two actively protected) were later

abandoned. The species' population decrease appears to be driven primarily by a decrease in the population of colonies located outside protected areas, whereas colonies established after 2003 fared better than older colonies (Table 3).

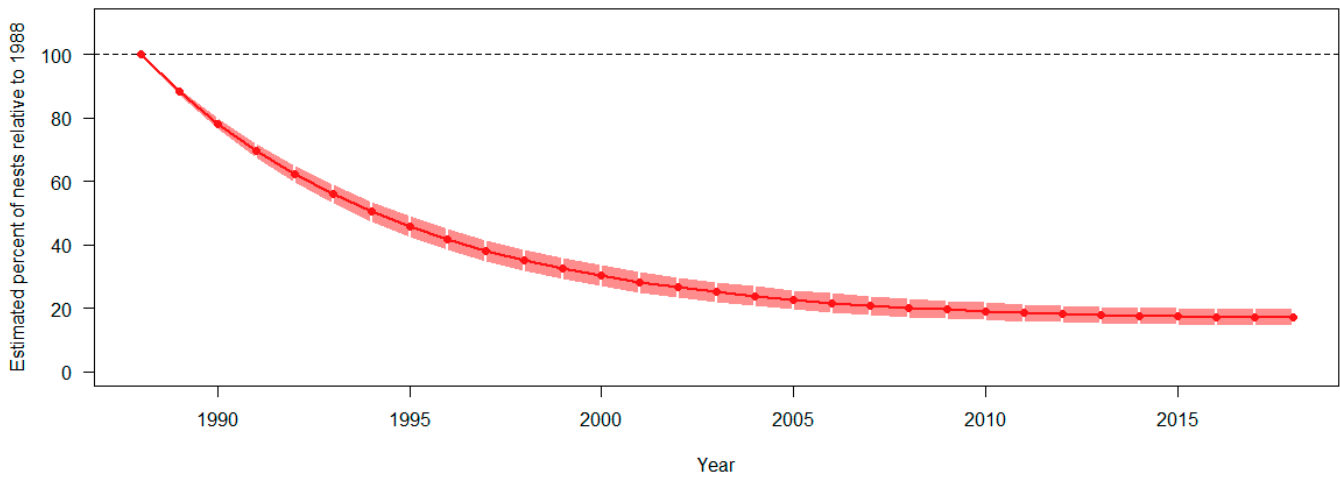


Figure 12. Nest population trend of the Grey Heron *Ardea cinerea* during the 1988–2018 period in Greece (moderate decrease). The red dots indicate the percentage of nests in a given year relative to the 1988 nest population, as estimated from the fitted model values of the best model (% of imputed values: 53). Dashed line marks the estimated percent of nests in 1988.

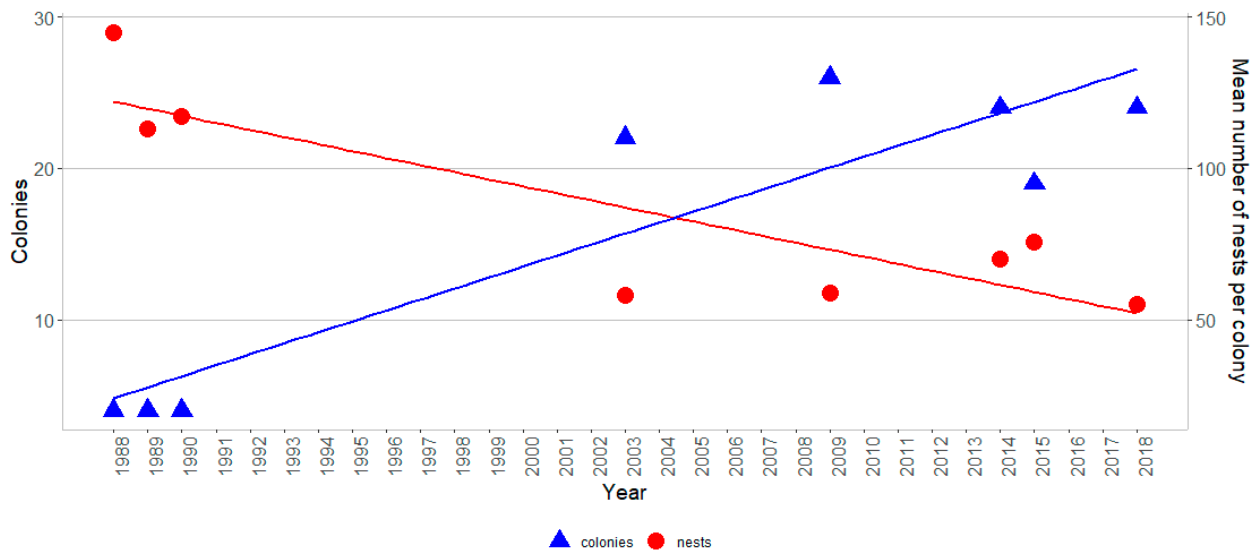


Figure 13. Changes in the number of Grey Heron *Ardea cinerea* colonies ($F = 29.47$, $df = 6$, $R^2_{adj} = 0.803$, $p = 0.002$) and the mean number of nests per colony ($F = 18.4$, $df = 6$, $R^2_{adj} = 0.713$, $p = 0.005$) during the period 1988–2018 in Greece.

3.7. Great White Egret (*Ardea alba*)

The species nested sporadically in Greece and in low numbers (one to five nests). In total, nests of the species were recorded in five wetlands (Kerkini Lake, Strymon River, Axios Delta, Volvi—Koronia Lakes, and Karla Lake, Figure 1). The highest number of nests ($n = 39$) was recorded in 2009 in one colony (Karla Lake). The discontinuous presence of the species in the national heron surveys meant that the species' population trend could not be assessed in the study period.

4. Discussion

4.1. Population Trend of Heron Species

The nesting populations of colonially nesting herons have fluctuated widely over the years both in Europe and worldwide. Factors such as climate/weather and land cover changes, water management, agricultural intensification, and changes in cultivation practices (especially for rice) are major drivers of these population fluctuations [3,4,6–8,31,32].

If we compare the observed population trends of heron species in Greece from this study to the overall trends in Europe, four species had a similar trend, the Cattle Egret (increase), the Little Egret, the Black-crowned Night Heron and the Grey Heron (decrease) ([33,34], Table A1).

The increasing population of the Cattle Egret in Greece—a species that established nesting populations during the study period—coincided with an expansion in Europe and globally [32]. Since the trend observed in our study is probably part of a continental scale range expansion, the local drivers of this expansion are similar to those reported in other countries; an increase in irrigated crops and pastureland ([11,33–35], Table A1).

The decline in the Little Egret nesting population in Europe (especially in Italy, Iberia, and Greece) is probably related to changes in rice cultivation practices, since a large proportion of the nesting population is near rice fields [11]. Rice fields are valuable substitute habitats for drained natural wetlands, as they support rich aquatic biodiversity. Many heron species establish their colonies close to rice fields where they forage, especially during the breeding period [36–39]. However, the chemical eradication of crop pests included in the herons' diet, such as the crustacean tadpole shrimp *Triops cancriformis*, and the adoption of new rice farming practices that require near-dry conditions, reduces the aquatic organisms that Little Egrets feed on [40] and, consequently, the rice fields' value as habitat for the species [7].

The current moderate decreasing trend we report for the Grey Heron in Greece agrees with the current trend for Europe overall according to the IUCN Red List (Table A1). It does not match, however, reports of the Mediterranean and Black Sea populations being stable according to Wetlands International [34] and increasing according to Keller et al. [33]. Moreover, the Grey Heron's decreasing population trend in Greece was continuous throughout the study period, unlike in Europe overall where the species' nesting population initially increased considerably after the 1980s due to the legal protection measures taken for birds [6,33]. The recent range expansion we report may be related to changes in the climatic conditions at the wetlands [33].

The European population trend of the Black-crowned Night Heron is decreasing according to Wetlands International [34] and Keller et al. [33] and stable according to the IUCN Red List (Table A1). The trends reported in other Mediterranean countries, such as Italy and France, were similar to the decreasing trend that we observed [6,7,27,41]. The European nesting population decrease for the species has been attributed to the loss and degradation of wetlands, anthropogenic disturbance near nesting colonies, and water pollution [33]. Additionally, as with the Little Egret, the population decrease is thought to be in part due to changes in rice field cultivations practices [7,11]. Furthermore, Fasola et al. [7,27] mentioned that the population decline could be driven by climate change in the species' overwintering areas in sub-Saharan Africa. Black-crowned Night Herons nesting in Italy and southern France overwinter in sub-Saharan West Africa and Sahel regions [42,43]. At least some of the Black-crowned Night Herons nesting in Greece also overwinter in sub-Saharan West Africa based on the recovery in Nigeria of an individual ringed in Greece [44].

The Purple Heron's European nesting population trend is disputed. According to the IUCN Red List (Table A1), it is increasing, while Wetlands International [34] and Keller et al. [33] support a decreasing trend, along with the eastern Mediterranean and Black Sea populations. The stable population observed in Greece represents only a small fraction of the European population, so it cannot resolve the debate.

The Squacco Heron's European nesting population trend is also disputed. According to the IUCN Red List (Table A1) and Keller et al. [33], overall, it is stable. However, Wetlands International [34] and Keller et al. [33] support the view that the south-western European population is increasing while the population in the eastern Mediterranean and the Black Sea is decreasing or fluctuating. Our results from Greece agree with Keller et al.'s [33] conclusion about the species' increasing trend in the region.

Discrepancies between the Greek Red Data Book and the IUCN Red List are most likely a result of scale-dependent changes in the listing and of access to different data [45]. Specifically, the smaller the area of assessment is, the smaller the population monitored, which in turn increases the chance of detecting the impact of local threats and therefore the chance of meeting red listing criteria for threatened species [45].

If we examine the colonially nesting herons in Greece overall, the number of heron colonies increased considerably during the study period. All species expanded their breeding range, primarily by creating new colonies at wetlands near existing colonies. Not all of the new colonies persisted over time though. Turnover was high for all species. There are several possible explanations for the observed range expansions. For example, the source ("old") colonies may have reached their carrying capacity in available nesting sites, while at the same time previously unsuitable habitat became available for nesting either via the creation/restoration of wetlands and/or increased protection (e.g., guarding). However, if these alone were the drivers for the range change, it would have been followed by an increase in the overall population. This was true only for two species (Squacco Heron, Cattle Egret). For three species (Little Egret, Black-crowned Night Heron, Grey Heron), the increase in number of colonies was accompanied by a decrease in overall population, while for the Purple Heron it was stable.

4.2. Drivers of Heron Nesting Population Trends

Several factors have been proposed as drivers of heron nesting population trends and shifts in nesting sites, such as climate and habitat changes (e.g., changes in land use or land management practices) affecting prey availability and nesting success, and disturbance levels at either the breeding and/or wintering grounds of the species [4,27,46].

Moreover, non-sustainable water management affected many freshwater bodies in Greece during the 1980s, 1990s, and early 2000s [47–50]. At the same time, water toxicity is thought to have increased in many wetlands with heron colonies as a result of significant long-term anthropogenic enrichment (e.g., phosphate fertilizers, waste, and sewage disposals—including heavy metals) [51,52].

Human disturbance was a threat to heron colonies in many wetlands since there was no systematic guarding of protected areas. The Forest Service, the government agency responsible for enforcing wildlife regulations in protected areas, had been focusing its resources primarily on forest habitats to combat activities such as illegal logging, leaving wetlands poorly patrolled. The situation improved only after 2003, following the establishment and staffing of Management Authorities for many protected areas (National Parks) by the Ministry of Environment and Energy. Park personnel started to systematically patrol wetlands, especially within the largest and most iconic national parks (e.g., Kerkini Lake). This, without doubt, contributed to the reduction in disturbance in many wetlands.

Additionally, colonies located within forest stands, woodland lots, or even single trees (e.g., Grey Heron colonies on plane trees) near agricultural land often experienced pressure from farming activities. The expansion of the agricultural land in some cases resulted in abandonment of colonies as nearby trees (or even trees with nests) were cut. The forest at Kerkini Lake, where one of the largest heron and Great and Pigmy Cormorant colonies was situated, has decreased dramatically in part due to the loss of standing trees caused by prolonged water inundation and low regeneration due to grazing [53]. This led certain species to shift their nests from the forest colony to nearby colonies or to experience a population decrease.

In this study, we examined the role of four parameters, namely whether the colony was: (a) within the Natura 2000 network, (b) within the area of operation of a protected area Management Authority (applicable only for counts after 2003; year the Management Authorities were first established), (c) within a new/restored wetland (i.e., did not exist prior to 2003), and (d) a new one (i.e., did not exist prior to 2003). Not all species' nesting populations responded in the same way to these parameters.

The effect of the Natura 2000 network could be inferred only for the three heron species with colonies both within and outside the protected area network (Little Egret, Squacco Heron, Grey Heron). The Grey Heron was the species with the highest percentage of colonies outside of protected areas, and those colonies fared worse in terms of nesting population trend compared to colonies within the Natura 2000 network. The importance of protected areas for the conservation of bird species is recognized [54,55], and most of the heron colonies in Europe occur within protected areas [4,11].

The effect of a colony being within the jurisdiction of an operational Management Authority on the species' population trend was significantly positive for the Black-crowned Night Heron and the Grey Heron. This suggests that the guarding effort by the park rangers succeeded in reducing at least some of the threats to these species to levels lower than at colonies not actively patrolled. Reduction in anthropogenic disturbance has been reported in Italy and Spain as a positive outcome of protected area for species including herons [6,56]. This is probably one of the reasons for the observed patterns in Greece. These benefits are not limited to herons, as similar population increases have been reported for other colonially nesting, wetland bird species in areas monitored by Management Authorities, such as the Spoonbill and Glossy Ibis [15,16], as well as large carnivores, such as the Brown Bear *Ursus arctos* [57] and the Golden Jackal *Canis aureus* [58]. However, the effect for the Purple Heron was inverse in our study, albeit not significantly. Since all Purple Heron colonies were located within sites with at least some level of protection (e.g., within a Natura 2000), this negative effect could reflect differences in the levels of afforded protection. Also, it emphasizes that certain human activities, such as poor water management practices, can affect even well-patrolled colonies by reducing habitat quality in surrounding (foraging) areas. Moreover, considering the Purple Heron's small number of nests per colony in national counts conducted after 2003 (range of 5 to 10 nests per colony), the year that the Management Authorities were established, the observed effect could be due to stochastic events in these colonies. In the case of the Cattle Egret, the location of a colony within a Management Authority was not an important predictor of the colony's nest population trend. This species started breeding in Greece mostly after 2003, the year that the Management Authorities were established, and mostly within protected areas. Therefore, there was no sufficient variation in the national survey sites for a pattern to be detected.

The creation or restoration of wetlands was positively related to the nesting population trend of two species, the Squacco and the Black-crowned Night Herons. This is an encouraging finding, as since the late 1980s, the country has embarked on a large-scale effort to reverse the drainage of most Greek wetlands that occurred during the interwar period (1920s–1930s) and to improve the quality of surviving ones, as even now many inland waters (especially lakes and rivers) are in poor condition [50,52,59]. In addition to wetland creation/restoration initiatives, there have been many campaigns aimed at raising public awareness of the need for wetland conservation. The largest wetland restoration project has been that of the Karla Lake in Thessaly, which was drained in the 1960s and was recently partially restored [22]. After the restoration of the lake, many waterbirds including herons, cormorants, pelicans, and Spoonbills started nesting there. Other successful wetland restoration or creation projects include the Koronia Lake, where decades of water mismanagement were addressed, resulting into two heron colonies being established there in 2015, and the Sani wetland (northern Greece), where a heron colony has been established. In addition to herons, other wetland species have also benefited from the new-restored wetlands, including Glossy Ibises, Spoonbills, and Great and Pygmy Cormorants [16,17].

Benefits to heron species from the improvement of wetlands have been also reported in other countries such as Spain [56], Sweden [60], and Finland [61].

The new heron colonies established during our study period (post-2003) may be smaller in size in relation to older/source colonies (with the exception of Cattle Egret colonies) but fared better in the case of three species; a higher population increase in the case of Squacco and Purple Herons, and a lower population decrease in the case of the Grey Heron. Such a pattern has been reported before, with new/small colonies having a higher level of breeding success in terms of successful nests and number of fledglings per nest compared to larger colonies [62]. Nevertheless, not all new colonies survived. Some collapsed after a few years. According to Kelly [63], the “life span” of the colony is closely related to the number of nests and the nesting species, and in most cases, new colonies are smaller than their source colonies [64]—as we observed in Greece. Overall, despite these colony losses, there was a net gain in colonies for all six heron species studied.

4.3. Management Measures

Despite the increasing breeding range of most species, our results show long-term decreasing population trends for three of the six heron species. It is therefore important that the general wetland restoration and specific colony conservation measures are maintained and—if possible—expanded in scale, so as to help reverse these trends. Emphasis should be placed on minimizing anthropogenic disturbance in protected wetlands and on improving foraging quality in habitats used by herons during the chick rearing season. Special attention should be given to the protection of small wetlands that could be used by herons for foraging. Moreover, the impact of modern rice farming practices—which increasingly involve draining the fields for days or weeks—on heron foraging should be investigated so that solutions can be found that both promote agricultural production and safeguard heron populations. The restoration of degraded wetlands should continue to be included in the national policy plans for nature conservation, which is in line with European Union’s carbon sequestration objectives to achieve a net zero carbon emissions economy by 2050. Special attention should also be given to the protection of riparian forests where many colonies are situated, and which, in some cases, are shrinking in size. It is imperative that a national waterbird survey plan is developed (including herons and other colonially nesting waterbirds) and the funding for its bi-annual implementation incorporated in the regular operation costs of the Natural Environment and Climate Change Agency, which oversees the management of all protected areas. Finally, there should be more research on the dietary needs of heron colonies in order to maintain high levels of breeding success. Such information is important for guiding wildlife and habitat management actions by the Management Authorities of the protected area.

5. Conclusions

Our study provides an overview of colonially nesting heron species at 65 colonies across 37 wetlands in Greece over three decades (1988–2018), raising awareness about the long-term declining breeding populations of three species and the role that 21st century wetland restoration and protection measures have had on heron colonies. The species with increasing trends in both breeding range and nest numbers were the Cattle Egret and the Squacco Heron—species that show similar trends across Europe. The declining breeding populations of Little Egrets and Black-crowned Night Herons could be related to recent “dry” rice cultivation practices, the impact of which on foraging habitat on herons should be closely studied and monitored. But herons breed also beyond protected areas, as is the case of the Grey Heron, and these colonies showed stronger decreasing trends in nest numbers during our study period. The importance and need for a systematic, nationwide survey of colonially nesting wetland birds—including herons—is supported by the results of this study, as it is a prerequisite for the successful management of both birds and their fragile wetland habitats.

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Conflicts of Interest: Author Nikolaos Bukas was employed by the company Plegadis Co. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Appendix A

Table A1. Conservation status of heron species in the IUCN RED LIST [65–71] and the Greek Red Data Book [9].

Species	Europe	Globally	Greece RDB
<i>Egretta garzetta</i>	<ul style="list-style-type: none"> IUCN Red List category: LC Current population trend: Decreasing Continuing decline of mature individuals: YES Population in Europe: 146,000 individuals 	<ul style="list-style-type: none"> IUCN Red List category: LC Current population trend: increasing Continuing decline of mature individuals: Unknown 	LC
<i>Nycticorax nycticorax</i>	<ul style="list-style-type: none"> IUCN Red List category: LC Current population trend: Stable Continuing decline of mature individuals: No Population in Europe: 137,000 individuals 	<ul style="list-style-type: none"> IUCN Red List category: LC Current population trend: Decreasing Continuing decline of mature individuals: Unknown 	NT
<i>Ardeola ralloides</i>	<ul style="list-style-type: none"> IUCN Red List category: LC Current population trend: Stable Continuing decline of mature individuals: No Population in Europe: 49,300 individuals 	<ul style="list-style-type: none"> IUCN Red List category: LC Current population trend: Unknown Continuing decline of mature individuals: Unknown 	VU

Table A1. Cont.

Species	Europe	Globally	Greece RDB
<i>Bubulcus ibis</i>	<ul style="list-style-type: none"> IUCN Red List category: LC Current population trend: Increasing Continuing decline of mature individuals: No Population in Europe: 164,000 individuals 	<ul style="list-style-type: none"> IUCN Red List category: LC Current population trend: Increasing Continuing decline of mature individuals: Unknown 	-
<i>Ardea purpurea</i>	<ul style="list-style-type: none"> IUCN Red List category: LC Current population trend: Increasing Continuing decline of mature individuals: No Population in Europe: 73,500 individuals 	<ul style="list-style-type: none"> IUCN Red List category: LC Current population trend: Decreasing Continuing decline of mature individuals: Unknown 	EN
<i>Ardea cinerea</i>	<ul style="list-style-type: none"> IUCN Red List category: LC Current population trend: Decreasing Continuing decline of mature individuals: YES Population in Europe: 583,000 individuals 	<ul style="list-style-type: none"> IUCN Red List category: LC Current population trend: Unknown Continuing decline of mature individuals: Unknown 	-
<i>Ardea alba</i>	<ul style="list-style-type: none"> IUCN Red List category: LC Current population trend: Increasing Continuing decline of mature individuals: No Population in Europe: 102,000 individuals 	<ul style="list-style-type: none"> IUCN Red List category: LC Current population trend: Unknown Continuing decline of mature individuals: Unknown 	VU

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